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October 1911

Editor: JOHN M. COULTER

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THE
BOTANICAL GAZETTE

OCTOBER 1911

AN ATTEMPTED ANALYSIS OF PARASITISM

D. T. MACDOUGAL

(WITH SIX FIGURES)

According to a recently published estimate made by the author, about half of the total number of seed plants use complex food material derived from other organisms by mycorhizal or parasitic arrangements. So far as our observations go, dependent species, which are advantaged by contact or association with other species, undergo direct somatic modifications, consisting chiefly of atrophies or reductions of the shoot and root system; and in plants of fixed parasitic habit, these reductions may be such as to include the total disappearance of the roots and to bring the shoot down to simple, unbranched, chlorophylless stems, upon which the leaves are represented by colorless bracts. The fruits and seeds may show various specializations.

During the course of an extensive investigation of the conditions under which two species may enter into the relation of host and parasite, regenerated cuttings of a large number of species were attached to the stems of desert succulents and xerophytes. In some cases the attached plants formed roots; and in others the epidermal cells performed the function of absorption.

The ruling factor was in all cases the osmotic ratio between the sap of the two plants; one plant may not become parasitic upon another except by the aid of a superior osmotic pressure which withdraws solutions from the tissues of the enforced host. Many causes, however, may operate to prevent a potential parasite

from becoming actual, such as the formation of wound-cork, excretions, periodic alterations in turgidity, etc. The physiological alterations consequent upon the arrangement of two plants in a xeno-parasitic relation are of a saltatory or mutative character, yet no evidence is at hand as to the manner in which such alterations become fixed and transmissible. A perfectly graded series of parasites may be selected which exemplify all stages of dependency, atrophies or reductions, and adjustive arrangements; but nothing may be assumed as to the manner in which progress has been made from one stage to another. It seems fair to conclude, however, that the evolutionary movement is generally toward increased dependency of the parasite, accompanied by accentuated and more complete atrophies. The view that such a movement may sometimes ultimately lead to extinction, although by a long and indirect way, seems also justifiable by inference, although such an end must not be assumed for all groups of parasites.

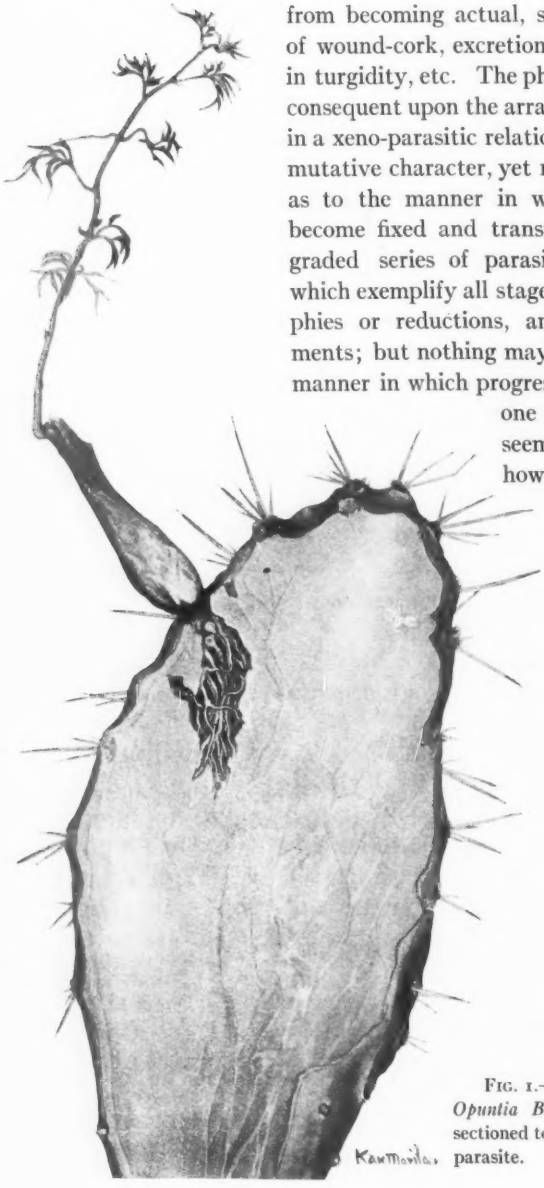

FIG. 1.—*Cissus laciniata* parasitic on *Opuntia Blakeana;* the host has been sectioned to expose the roots of the xeno-parasite.

In the experiments carried on at the Desert Laboratory from 1908 to 1911, the desert grape (*Cissus laciniata*) of Mexico, the expressed juice of which shows a pressure of over 11 atmospheres, was found to maintain itself on the flattened joints of *Opuntia Blakeana* at about 9 atmospheres; not so successfully on *Echinocactus Wislizeni*, the drinkable juice of which has a concentration equivalent to about 6 atmospheres; while it soon perished when attached to stems of the great tree cactus (*Carnegiea gigantea*) at less than 7 atmospheres (fig. 1). The last named plant exudes an acrid fluid from fresh wounds, which are quickly closed by the formation of heavy, corky layers. *Opuntia versicolor*, a species with cylindrical stems showing a pressure of 12 atmospheres, was able to draw supplies for extended periods from *Carnegiea* and the other hosts mentioned. Plantlets of *Agave* were equally efficient, although this xeno-parasite formed such a great number of roots as to destroy the tissues of the host plant. *Cissus* also formed roots which penetrated the host, while the absorptive contact of *Opuntia* (flat-stemmed) was by the epidermal cells of the stems in every case examined.

The briefest inspection of the results of the analysis of plants used in these experiments, shows that the direct proportion of mineral salts in the sap and the acid contents of the sap have no direct bearing on possible parasitism among the higher plants.[1] The relation of seasonal cycles, capacity for development of absorptive elements *de novo*, and an accommodative adjustment of the osmotic pressure of the cell sap are to be mentioned as factors in the making of nutritive couples. The greater number of the parasitic arrangements made are to be included with the root parasites.

A few additional experiments were set up to test certain points after the completion of the manuscript printed in 1910. The results of these and of the continuation of older preparations seem to warrant the presentation of this additional note on the subject.

May 11, 1910.—A number of beans of a mixture of species native to the deserts of southern Arizona were attached to joints

[1] See MACDOUGAL and CANNON, The conditions of parasitism in plants. Publ. No. 129, Carnegie Inst. of Wash. 1910.

of prickly pear, with the radicles thrust into cavities in the soft tissue. The bean was held in place by a setting of plaster of Paris, and a moist strip of cloth was brought from a vessel of water to furnish moisture until the plants should become established in their new relations.

May 13.—A large number of new insertions of the "rusty" bean in joints of *Opuntia* and bodies of *Carnegiea* and *Echinocactus* were made on this day. Some of the original preparations were showing notable growth.

May 14.—Some of the plants first arranged had thrust the tips of the plumules beyond the cotyledons, but had not yet straightened the hypocotyl. One bean with wilted plumule was taken out of the *Opuntia*. The main root had grown but little. A secondary branch from near its base had come out and extended down into the cavity, alongside the main root, showing as great a length.

May 22.—Twelve seedlings on *Opuntia* had survived, of which one had developed the plumule to an extent that the leaves were unfolding from between the cotyledons. Six seedlings on *Echinocactus* had survived, and were showing some slight development. Three seedlings out of 9 insertions on *Carnegiea* had survived and had made a slight development. The cotyledonary curvature was still markedly present.

May 31.—Temperatures of 111° and 112° F. out of doors, and all parasites were flagging, apparently dying. All soon perished.

About a dozen germinated beans of the form known as "small Papago white" were inserted in joint of "Mission Pear" (*Opuntia* sp.), near the laboratory at Carmel, California, on June 23, without any protection except a cloth shade. These, with the exception of two, dried out, although small secondary roots were formed by June 27. All were replaced and a small vial was arranged with a strip of cloth to give shade and moisture. About 8 similar preparations were arranged on *Oenothera biennis* and *O.H.206*. On July 1, only one of this lot had become dry, the fogs of the preceding days having been an obvious advantage.

July 14.—Seven Papago white beans on Mission Pear thriving, of which three had well developed leaves of the first simple pair.

and one showed a second pair. The others still retained the plumule partly between the cotyledons.

August 2.—All beans were dead or nearly so. All of the development in these plants was undoubtedly carried on at the expense of material in the cotyledons; and the roots soon perished after being immersed in the mucilaginous tissues of *Opuntia* or the stems of *Oenothera*. The high humidity of the fogs and low temperatures ranging between 45° and 65° F. also made for the endurance of the seedlings. These tests are chiefly interesting in contrast with the cultures of PEIRCE, in which plants of *Pisum sativum* were grown on stems of *Vicia Faba* to maturity. The advantage of the aeration of the roots in the central cavities of the stems of the host and also of one legume parasitic upon another, doubtless accounts in large measure for the success of these cultures.[2]

The completion of the original manuscript on this subject left several preparations in good condition, which were two years old. Among these were *Opuntia Blakeana*, *O. versicolor*, *O. arbuscula*, and *O. leptocaulis* on *Carnegiea; O. leptocaulis* on *O. discate;* also one *Agave americana* on *Carnegiea*. Some of these parasites remained alive throughout a part or all the year, it being noted that those shielded from direct illumination by the body of the host survived longest. March 1911 found arrangements of *Opuntia versicolor*, *O. Blakeana*, and *Agave* on *Carnegiea*.

All these preparations were made with plants as xeno-parasites which were characterized by a water balance of some amount and by an osmotic pressure of the sap of 9–12 atmospheres. Furthermore, the survivors were held in place by a mass of plaster of Paris molded about the bases of the stems which held the roots closely appressed against the corky tissues of the host.

This state of affairs may be seen to furnish a fair approximation of the physical conditions under which an *Opuntia* was found with the roots in a small cavity in the trunk of a *Parkinsonia*, and of the same species in a cavity in the summit of a trunk of *Carnegiea*.[3] A further illustration is offered by a case photographed and reported

[2] PEIRCE, G. J., Artificial parasitism, etc. BOT. GAZ. **38**: 214. 1904.

[3] See Publ. No. 129, Carnegie Inst. of Wash. 1910.

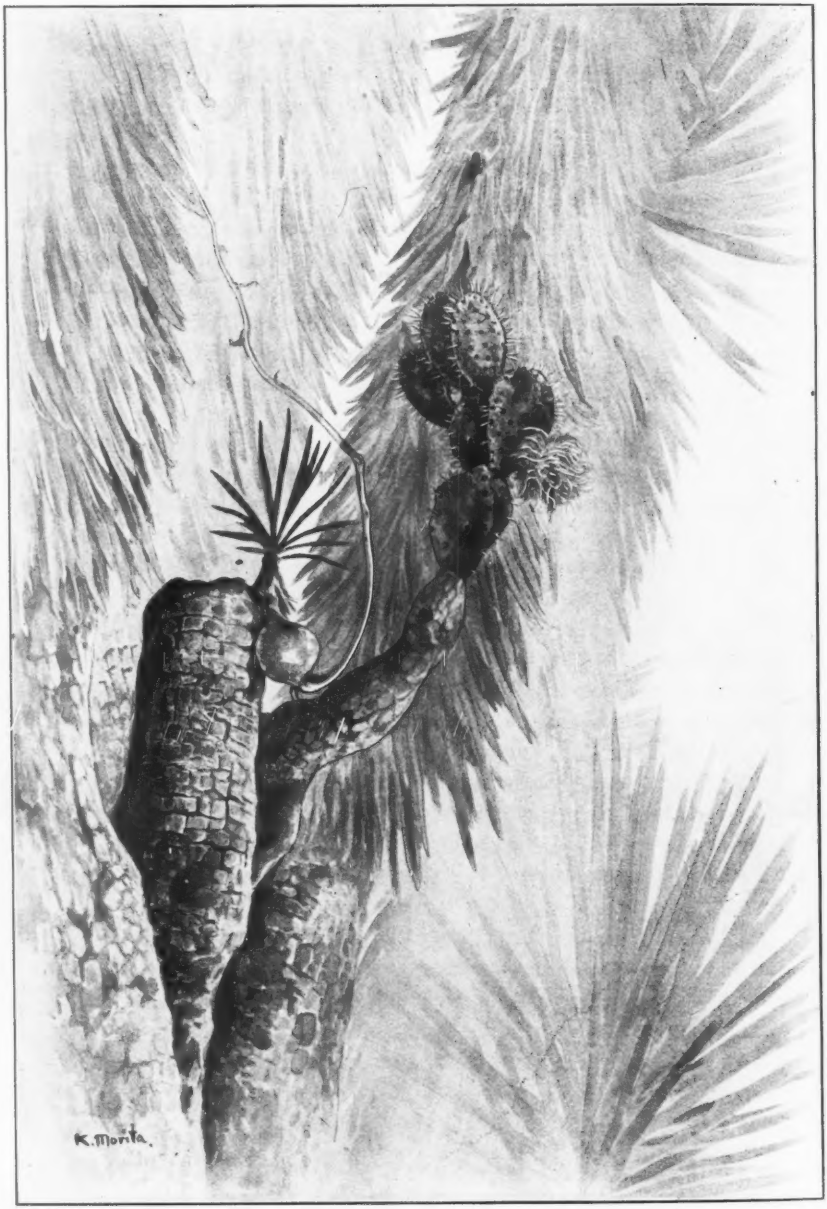

FIG. 2.—*Cissus laciniata* and *Opuntia* growing from sinus in stem of *Yucca*, near Tehaucan. Mex.; an epiphytic bromeliad is attached to one of the terminal joints of the *Opuntia*.

by Dr. W. A. CANNON, in which a flat-jointed *Opuntia* was found established in a cavity in the trunk of an *Acacia Greggii*. One or more species of *Opuntia* native to the Tehuacan region find a foothold in the crevices of tile roofs, and stone and adobe walls, in a very noticeable manner; and it was in this vicinity that one of these plants and a native grape were found rooted in the sinus of a forked tree *Yucca* (fig. 2).

The conditions of such association seem favorable for the slow extraction of solutions from the host plant through non-living tissues without the actual contact of the living cells, an approximation to the initial conditions of parasitism. It is obvious that the crowded root systems of a wide physiological variety of plants in the soil furnish numberless duplications of these conditions, and it seems entirely reasonable to suppose that such contiguity of absorbent and succulent roots may acccount, in part, for the greater number of root parasites.

It is to be noted that among the higher plants the part played by destructive secretions is at a minimum. The activity or absence of such substances in seed parasites has been variously described. In no instance, however, are there such abundant and disintegrating effects as may be seen resulting from bacterial and fungal parasites of plants and animals.

The parasitic arrangements described above, in which the host furnishes lodgment and a slowly yielded supply of solution, are characterized by a slow growth of the parasite, in which the amount of development is limited, the members being reduced. The *Opuntia* parasitic on *Parkinsonia*, which was described in *Publication No. 129*, Carnegie Inst. of Washington, 1910 (see pl. 10), was taken from the host early in 1910 and set in the adobe soil of the terraces in the courtyard of the Desert Laboratory. In the course of the growing season of that year, it made three new joints, each of which was three or four times the bulk of those previously formed, the total growth in the previous 7 or 8 years. Furthermore, in this autophytic growth it developed characters which demonstrated that it properly belonged to *Opuntia Toumeyi* instead of *O. Blakeana*, with which it was first identified, because of its small joints and atrophied spines (fig. 5).

The *Opuntia versicolor* which had been fastened in a cavity in the side of a tall *Carnegiea* early in 1909, lost three of its four short branches and the terminal section of the stem during the dry foresummer of 1910. Activity in the rainy season in the midsummer following resulted, not in the formation of additional sections or members, but in the increase in thickness of the stem

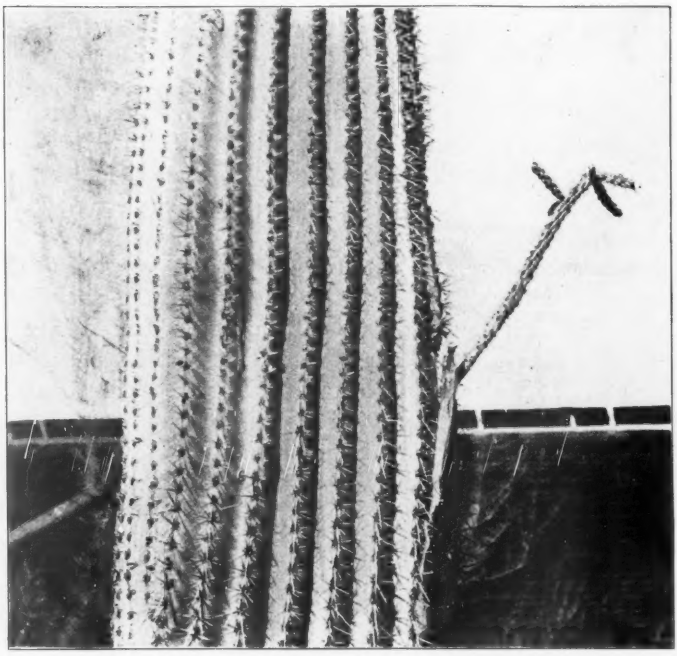

FIG. 3.—*Opuntia versicolor* parasitic on *Carnegiea gigantea*, March 1910

and roots; the latter were thin and fibrous when the preparation was made, January 23, 1909. After two years of parasitic existence, the visible portions of the root system were much enlarged, after a manner sometimes exhibited by autophytic individuals of the same species (figs. 3 and 4).

An *Opuntia Blakeana* set in a cavity of *Carnegiea*, where it was held by plaster, early in 1909, likewise formed no additional

members during the following two years. Some thickening of the cylindrical basal segment, however, was noticeable.

The work described in this and previous papers has been successful in the demonstration of certain physical conditions which make parasitism possible, and has led to the suggestion of physiological activities which limit or facilitate the adhesion of two seed plants in a dependent nutritive combination. Wider observations would doubtless increase the known parasitic combinations, while it may be safely assumed that present conditions are as favorable for their making as at any time in the history of the plant world. New parasites may be expected to be brought to our attention from time to time.

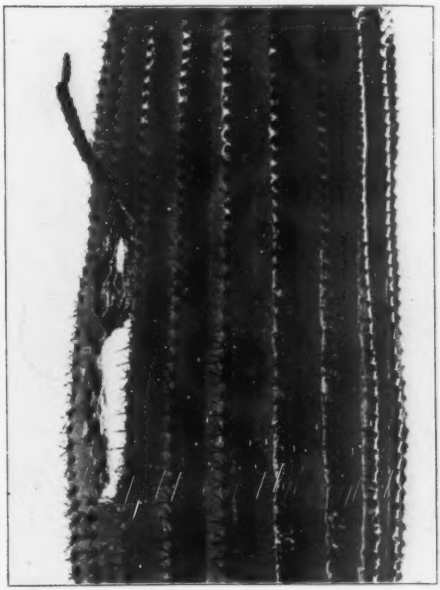

FIG. 4.—Same plant as in fig. 3, March 1911, with enlarged roots and stem, and with but one surviving branch.

The assumption of a mutualistic or dependent rôle, in fact any departure from a purely autophytic condition by a green plant, is inevitably followed by reductions or atrophies. Such combinations are displayed by a number of seed plants, not far short of half the existing species. It is of interest to note that the parasitical consequences have not yet been seen in green plants furnished with food material including organic compounds. The total reaction is complex, and the exciting causes are probably not simple. Whatever they may be, they are furnished only by the living or decaying bodies of other organisms. The part played by the pathological effects and physiologic reactions of parasites in

the evolutionary development of plants has never been adequately portrayed, even in a speculative manner.

The vigor of growth, widely varied capacity for reproduction, range of endurance to unfavorable conditions, and accommodational adjustment displayed by parasitic fungi and bacteria in general seem to place the greater majority of these forms in a

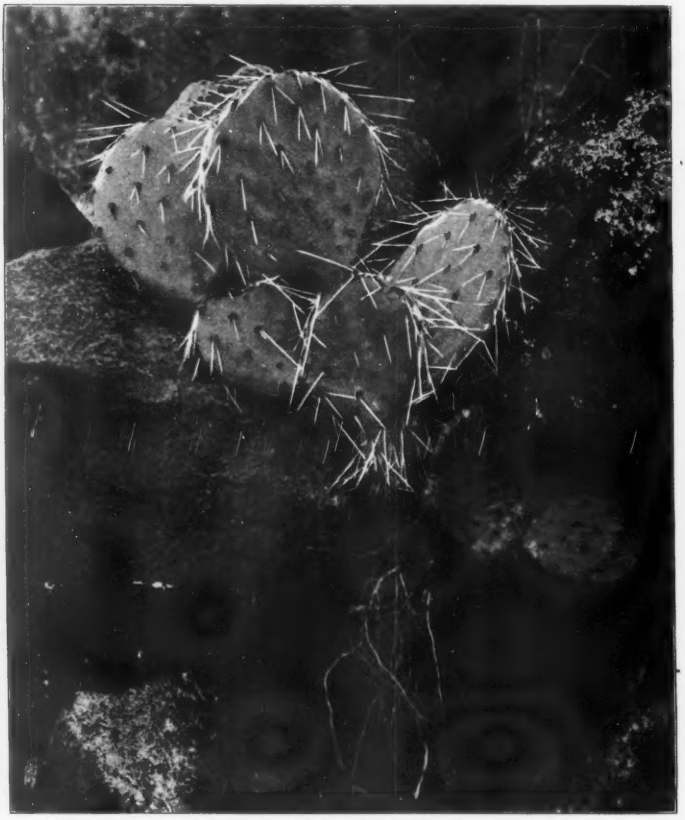

FIG. 5.—*Opuntia Toumeyi;* this plant was found growing in a cavity of the trunk of a small tree of *Parkinsonia microphylla* in 1906, and the small joints formed during its parasitism are to be seen near the base and to the right; the larger joints were developed after the plant began an autophytic existence rooted in the soil; photographed February 1911.

position where the only obvious way to extinction would be by the destruction of their hosts, resulting from their own effectiveness. Nothing known of the life history of any of these forms suggests a possible abandonment of the parasitic habit and of an advancing morphological development. So far as the higher plants are concerned, the only consideration hitherto given to parasitic forms has been to view them as passing down an inclined plane of atrophies, which would ultimately lead to their extinction, without reference to the abundance of development of the host forms. No hint has yet been obtained as to the possibility of a retracement, by which a dependent might once more regain its standing as an autophyte.

FIG. 6.—*Cissus laciniata* parasitic on *Opuntia Blakeana* (see fig. 2).

Regressive action of this character would naturally be discernible only in a series of material extending over long periods of time, such as that obtained by the paleontologist. It is interesting to note that this subject is one to which some serious attention has been given, and Dr. J. M. CLARKE[4] has recently summarized the information with regard to the case of the limpet and the

[4] The significance of certain early parasitic conditions. Science **33**: 291. 1911.

crinoid of earlier times and the gastropods and sea urchins of the present. It is made clear by CLARKE that the limpets of the early Silurian were largely parasitic on the crinoids, a habit that persisted for millions of years, until the closing stages of the Paleozoic, when evidences of it were lost, and no traces of parasitism of snails on the few crinoids of the present are known. Other gastropods of the limpet structure are now parasitic on the starfish and sea urchins, close relatives of the crinoids. The earlier limpets were not carried beyond the stage of possible regression in their parasitism, but the modern parasitic gastropods are "often so modified by their degeneracy that their nature is hardly recognizable, and this parasitism is fixed and beyond repair." Two separate cases of adaptational adjustments seem involved, and the parasitism of the modern gastropods is taken to be wholly independent of the earlier assumption and abandonment of the habit. The suggestion lies near, however, that a family which has thus furnished two separate series of parasites is one which by morphological characters or physiological tendencies is liable to assume dependent relations with other organisms as hosts. Parasitism among the higher plants of the present time is confined to ten families, one of which has been added recently to the list by the work of Dr. W. A. CANNON. It may be safely assumed that in some of these, the Orobanchaceae, for example, the habit is far beyond retraction.

DESERT LABORATORY
TUCSON, ARIZONA

CONTRIBUTION FROM THE ROCKY MOUNTAIN HERBARIUM. IX

NEW PLANTS FROM IDAHO

AVEN NELSON

Most of the plants considered in this paper were collected in Idaho. Since they were secured during a single season by an amateur, a word concerning the collector and the field investigated will not seem out of place. Early in 1910 specimens were received from J. FRANCIS MACBRIDE for determination. In the correspondence that developed it was soon apparent that he was a close observer and deeply interested in the flora of his neighborhood and state. A proposition from him to collect for the Rocky Mountain Herbarium led to the discovery that he was a boy just out of the Boise High School. An agreement was soon reached whereby he was to undertake field work in some part of Idaho.

To determine the least worked and therefore the most inviting field, appeal was made to the two men who probably know the flora of the state better than any others, namely the former professor of botany at the University of Idaho, L. F. HENDERSON, and Professor ELIAS NELSON of the Experiment Station. These were agreed that southwestern Idaho was practically unexplored, particularly the whole Owyhee region including the mountains of that name. Their judgment has been confirmed by the work thus far carried out, and further collections in this very interesting field will be made in 1911.

ERIOGONUM OVALIFOLIUM Nutt.—As the collections of this so-called "aggregate" species multiply, the probability increases that the seemingly quite distinct forms of it represent but one very variable species. The type of the species was the comparatively small yellow-flowered form. Then NUTTALL gave us *E. purpureum*, differing in no respect except in color. It has since been shown that between the two the specimens show all shades of yellow to white, and white to purple. At most then, NUTTALL'S second species

ought not to be recognized as more than a variety, and as a recognizable though not necessarily permanent variation.

What is true of *E. purpureum* Nutt. is equally true of three of SMALL's segregates. They are based on no permanent characters, since in this genus color and size have been shown to vary with every change in the ecological factors. Two of these species, *E. ochroleucum* and *E. orthocaulon*, occur in the semi-arid portion of the Snake River basin and its tributaries. They may grow intermingled in the same district, as was the case in the superb specimens mentioned below. I therefore propose one varietal name to represent the two as follows.

ERIOGONUM OVALIFOLIUM **celsum.**—*E. ochroleucum* Small, Mem. N.Y. Bot. Gard. **1**:123. 1900; *E. orthocaulon* Small, Bull. Torr. Club **33**:53. 1906.

MACBRIDE'S specimens, soon to be distributed under this varietal name, represent well the two colors, the oval to oblong leaves, and the tall scapes. New Plymouth, Idaho, May 21, 1910, nos. 85 and 86.

ERIOGONUM OVALIFOLIUM **vineum.**—*E. vineum* Small, Bull. Torr. Club **25**:45. 1898.

Besides the wine-colored flowers, this is more noticeably tomentose, hence may be kept distinct from the preceding variety, though like that it merely represents the species in its maximum development.

Stanleya rara, n. sp.—Inflorescence inordinately crowded, becoming 4 or more dm. long, the rachis only moderately stout: pedicels about 10 mm. long, in fruit 15–20 mm.: sepals yellow, linear, about 10 mm. long and 1 mm. or more wide: petals yellow, linear, narrower than the sepals and about three times as long; the claw longer than the sepals and but little narrower than the blade: anthers 3–4 mm. long, at length well exserted and more or less curved or coiled: ovary at full anthesis about 4 mm. long, somewhat shorter than its stipe: pods at maturity filiform, 4–6 cm. long or possibly more, irregularly curved and spreading, on stipes nearly half as long and somewhat longer than the pedicels.

This is a tentative description of a seemingly excellent species, and is described from only a fragment of the plant. This had been gathered for a bouquet by Mrs. CROUTHERS, on a dry hillside, near Big Willow post-office, in Canyon Co., Idaho, about May 25, 1910, where it undoubtedly is indigenous.

This fragment is no. 217 in MACBRIDE'S series. He will try to secure the plant in quantity in 1911.

Thelypodium milleflorum, n. sp.—Tall, branching, wholly glabrous, biennial, 1–2 m. high, the stout main axis and the much slenderer ascending branches a deep purple below, becoming paler upward: leaves coarsely and irregularly dentate to entire, passing from oblong below to linear above; the lower petioles 6–15 cm. long, usually shorter than the blades, becoming shorter upward: inflorescence greatly crowded, at length very long (that of the main axis often 4–6 dm.) but even in fruit quite dense: flowers, pedicels, and even the rachis very pale or milky white: sepals narrowly oblong-linear, slightly cucullate and greenish at the tip, about 5 mm. long: petals very narrow, twice as long as the sepals; the spreading blade nearly linear: the clawlike portion filiform but distinctly expanding again near the base: filaments at length well exserted, and the purple, linear, scarcely sagittate anthers coiled: pods a pure green, in good contrast with the pale pedicels and rachis, almost filiform, 6–10 cm. long, normally strongly ascending or suberect, but often irregularly spreading as if from their weight: stipe 2–3 mm. long; the style about the same length: the ascending pedicels a little longer than the stipes.

This is *T. laciniatum* Endl. in part, some specimens being found in herbaria under that name. That species differs from this in many ways, but noticeably its habitat (on rocks), its smaller size, its laciniate leaves, its shorter, thicker, spreading pods, and opener inflorescence with green pedicels and rachis.

The best specimens are MACBRIDE 234, New Plymouth, Idaho; abundant in rich soils on open slopes; in May, and by June in full fruit. It is also represented by CUSICK 1955, from dry bottom lands, Malheur Co., Oregon; BAKER 1020, Eagle Valley, Ormsby Co., Nevada; COTTON 391, Yakima region, Washington.

RORIPA PALUSTRIS (L.) Bess.—In studying MACBRIDE'S collections, I found a variation of this widely dispersed species that is quite noteworthy. This led to an examination of all the available specimens at hand, as well as of those representing what we have been calling *R. hispida* (Desv.) Brit. In this study it became evident that MACBRIDE'S specimens have the size, habit, and general aspect, and the perfect glabrateness of *R. palustris*, but

the globose or subglobose pods of *R. hispida*. One is therefore driven to the conclusion that these are but variations of one species.

In the present disturbed condition of nomenclature, one scarcely knows what generic designation to employ. However, if one ignores names prior to 1753, the order of the three names commonly employed seems to be *Roripa* Scop., Fl. Carn. 520. 1760; *Radicula* Dell. ex Moench, Meth. 262. 1794; *Nasturtium* R. Br. Ait., Hort. Kew. Ed. 2. **4**:109. 1812.

Following the same plan on the specific name it seems to result as follows:

Roripa terrestris (R. Br.), n. comb.—*Nasturtium terrestre* R. Br., *l.c.*; *N. palustre* DC., Syst. **2**:191. 1821; *Roripa palustris* (L.) Bess., Enum. 27. 1821.

RORIPA TERRESTRIS **hispida,** n. comb.—*Brachylobus hispidus* Desv., Journ. Bot. **3**:183. 1814; *Nasturtium hispidum* DC., *l.c.*; *Roripa palustris hispida* Rybd., Contrib. U.S. Nat. Herb. **3**:149. 1895.

RORIPA TERRISTRIS **globosa,** n. var.—Tall and often declined, 4–10 dm. high, perfectly glabrous; pods globose or subglobose, with a short necklike constriction between pod and receptacle.

MACBRIDE 275 is typical; swampy land, Falk's Store, Canyon Co., Idaho, June 22, 1910: also by AVEN NELSON, Head of Wood's Creek, Albany Co., Wyoming, August 1910.

Spiraea idahoensis, n. sp.—A shrub, wholly glabrous throughout, 10–18 dm. high, branched below; the current year's branches erect, 3–5 dm. long and very leafy: bark of young branches very pale reddish brown: leaves large, ovate to elliptic or often oval, usually rounded-obtuse at both ends but sometimes subacute at apex, nearly regularly serrate often almost to the base, 5–9 cm. long: panicle large, more or less compound, cylindrical or pyramidal, the lower branches of the panicle axillary to the uppermost somewhat reduced leaves: calyx lobes reflexed, triangular-ovate, mostly acute, about as long as the disk: petals rose color, about 2 mm. long, twice as long as the calyx lobes, ovate, subacute or obtuse: filaments slender, more than twice as long as the petals: carpels ovate-oblong, smooth and polished, about 0.5 m. long.

It is singular that this Idaho shrub should so long have passed for *S. Menziesii* Hook. That species finds its typical development along streams and

in cold bogs of the Northwest. It is always more or less pubescent, and its leaves are typically narrower and smaller. Its Idaho counterpart is a shrub of the mountains or foothills, in moist soil but not in marshy or wet places. *S. idahoensis* is reported plentiful throughout southern Idaho.

The type is MACBRIDE 630, collected at Trinity, Elmore Co., August 23, 1910.

Potentilla trina, n. sp.—Perennial from a rough shreddy but slender vertical caudex, 4–8 cm. long, green and glabrate or even quite glabrous: stems less than 1 dm. high, slender but erect, few-leaved and few-flowered: leaves trifoliate: basal leaves on slender petioles 5–8 cm. long; leaflets short-petioled or subsessile, 1–3 cm. long, broadly obovate-cuneate, deeply and incisely toothed, the teeth more or less incised; stem leaves sessile, narrowly cuneate, incisely toothed at apex: cymes very few-flowered: calyx tube sparsely and minutely hirsute; sepals triangular-lanceolate, about 5 mm. long, acute, obscurely ciliolate; bractlets oblong, mostly obtuse, shorter than the sepals: petals obovate, emarginate, 6–8 mm. long: stamens about 20: carpels 20–25.

This is a very near relative of *P. emarginata* Pursh, and may be only a geographical variety of that arctic species. If it stands as a species, it must do so on the strength of its almost glabrate condition, larger and longer rootstocks, larger leaflets, and erect habit.

Collected by MACBRIDE in the Trinity Mountains, on the grassy banks of Star Lake, one of the Trinity Lakes, August 30, 1910, no. 680. Only a few plants were found.

Prunus padifolia, n. comb.—*Cerasus padifolia* Greene, Proc. Biol. Soc. Wash. **18**:59. 1905.

MACBRIDE secured some excellent red cherry specimens on his collecting trip in Idaho in 1910. These led to an examination of GREENE'S interesting paper on "Some West American red cherries." A checking up of the specimens in the Rocky Mountain Herbarium in the light of this paper revealed some sheets referable to the above name, including MACBRIDE 443 and 479 from Silver City and Twilight Gulch. He secured two sets of specimens, one typically red-fruited, the other with fruit a clear lemon yellow. Otherwise no differences in the two collections could be seen. A character not mentioned by GREENE is the glandular denticulation of the leaf margin.

Thermopsis xylorhiza, n. sp.—Stems clustered, erect, rather slender, from a branched woody caudex surmounting a stout woody root, 4–7 dm. high, simple and (at maturity) leafless below, sparingly branched above, glabrate and somewhat striate: green,

glabrous above, very sparsely pubescent beneath; the stipules ovate or obovate, obtuse or acutish, 2–4 cm. long, either longer or shorter than the petiole; leaflets oval to narrowly elliptic, obtuse or acutish at apex, mostly somewhat cuneate at base, 4–8 cm. long: raceme of 10–20 rather crowded flowers; calyx finely pubescent; the campanulate tube 6–7 mm. long, the triangular acute teeth half as long; the deep-yellow corolla more than twice as long as the calyx: the young pods erect, straight, white with fine silky pubescence, at maturity greenish and sparingly pubescent, moderately or only slightly arcuate, spreading, 4–8 cm. long and 5–7 mm. broad; the pedicels 5 mm. or less.

So far as known to the writer, the other western species all have a semi-fleshy running rootstock, but aside from the woody character of the caudex and roots this species has other good characters to distinguish it.

Secured by MACBRIDE at Falk's Store, Canyon Co., Idaho, May 24, 1910, no. 99.

Hypericum tapetoides, n. sp.—Depressed perennial, spreading by the slender rhizome-like stems which root at the nodes, very leafy: leaves glabrous, oval or obovate, tapering to the half-clasping base, 5 mm. or less long, longer than the internodes: flowers rarely solitary terminal, usually in cymes of 3–several: sepals 5, similar, narrowly elliptic-oblong, abruptly acute, about 3 mm. long: petals 5, orange yellow, elliptic, very delicate, 5–7-nerved, as long as or longer than the sepals, marcescent: stamens 12–20, distinct, nearly as long as the petals: styles 2–4, equaling the stamens, slightly dilated upward to the truncate or subcapitate summit: capsule ovoid, acute, as long as the sepals: seeds numerous, oblong, minutely longitudinally roughened striate.

Very distinct from *H. bryophytum* Elmer, BOT. GAZ. **36**:60. 1903, and from *H. anagalloides nevadense* Greene, Fl. Fran. 113, apparently the only species to which it makes a close approach. It was found growing in dense mats on sunny mossy, boggy stream and lake banks, usually intermingled with mosses and with these forming thick soppy-wet carpets of green. MACBRIDE 453, Silver City, Owyhee Mountains, in bloom, July 22; no. 570, Trinity, Elmore Co., in fruit, August 1910.

SPHAERALCEA RIVULARIS **diversa,** n. var.—Differing from the species in the green and almost glabrous leaves which are shallowly only 3–5-lobed; the lobes mostly obtuse, often broadly rounded,

never sharply serrate on the margin but varying from entire to merely undulate crenate: flowers not crowded-terminal as in the species, but axillary-pediceled in the upper leaves and in a short nearly naked terminal raceme of 3 or 4 flowers: carpels hirsute-hispid on upper part of the back only.

MACBRIDE 582, moist hillsides, Manyon Creek, Elmore Co., August 11, 1910.

Phaeostoma rhomboidea, n. comb.—*Clarkia rhomboidea* Dougl., Hook. Fl. Bor. Am. **1**:214. 1833; *Opsianthes gaurioides* Lilja, Linnaea **15**:261. 1840.

The genus *Phaeostoma* was established by SPACH (Hist. Veg. Phan. **4**:392. 1835), one species being referred to it, namely *P. Douglasii*, which was the earlier *Clarkia elegans* Dougl. I am not so much surprised that this excellent genus was later suppressed (during the Benthamian era) as I am that it has not been since restored. There are only a very few species referable to it, but these are so aberrant in the genus *Clarkia* that one trying to find them by means of keys now available meets with a number of contradictory and misleading statements. *Clarkia rhomboidea* runs just as readily to *Godetia* as to *Clarkia*, for it requires a decided mental bias to recognize the narrowed base of its petals as a claw.

Removing the species with entire petals from *Clarkia*, it becomes homogeneous in that all the species have clawed, 3-lobed petals, only 4 real stamens, and a stigma evidently lobed. *Phaeostoma*, on the other hand, has entire petals with or without claw, eight perfect subequal stamens, and a stigma with lobes so short that the stigma looks capitate or disciform. It is to be noted too that in *Phaeostoma* some of the leaves are opposite. The other species referable to this genus are as follows:

Phaeostoma elegans, n. comb.—*Clarkia elegans* Dougl., Lindl. Bot. Reg. *t. 1575*.

Phaeostoma xanthiana, n. comb.—*Clarkia xanthiana* Gray, Proc. Bost. Soc. Nat. Hist. **7**:145. 1861.

Phaeostoma parviflora, n. comb.—*Clarkia parviflora* Eastwood, Bull. Torr. Club **30**:492. 1903.

Sphaerostigma implexa, n. sp.—Annual, more or less branched from the base and upward, 1–2 dm. high; the stems and branches puberulent and purplish tinged, the bark not exfoliating; the branches ascending, almost as long as the main axis: leaves glabrate or puberulent, oblanceolate to oblong-lanceolate, tapering to a short petiole; the lower 5–7 cm. long, upward passing into the

narrow bracts which are gradually reduced; raceme crowded, becoming narrow and more or less secund, puberulent: calyx lobes lanceolate, 5–6 mm. long, and about twice as long as the tube: petals greenish- or yellowish-white, suborbicular, abruptly acutish, or with a tooth on the subtruncate apex, as long as the calyx lobes: capsule narrowly linear, subcylindrical and only slightly enlarged downward, at maturity 20–25 mm. long and greatly contorted or implexed.

The habit and general appearance of this suggests *S. decorticans* (H. & A.) Small, from which it is far removed geographically and otherwise.

Type, MACBRIDE 27, from Falk's Store, Canyon Co., Idaho, dry stony hillsides, May 17, 1910.

Onagra (OENOTHERA) **ornata,** n. sp.—Stout biennial, widely spreading from the summit of a rather large woody root; the several stems assurgent and simple, 5 dm. or more high, very leafy, densely and finely pubescent, with some scattering ciliate hairs: leaves narrowly oblong-lanceolate to linear-lanceloate, the largest 10–14 cm. long, reduced toward the base and into the bracts (first year leaves not seen), with short dense subcinerous pubescence: inflorescence crowded: calyx densely white hirsute-pubescent, at anthesis its tube less than 4 cm. long, about twice as long as the ovary, its lobes as long as or longer than the tube: corolla a deep golden yellow, unchanged in drying or shading to orange; the petals broadly triangular-obovate or obcordate, as long as the calyx lobes: anthers yellow, 12–15 mm. long; the filaments much shorter than the petals: style not protruding from the bud but elongating and surpassing the stamens as the buds open: capsule pubescent, 2–3 cm. long, somewhat thickened on the angles and only slightly tapering: seeds angled.

This highly beautiful evening primrose, coming as it does from a state supposedly fairly well worked, is a distinct surprise. Doubtless, however, it is an indigenous plant. The excellent key prepared by Dr. R. R. GATES (Mo. Bot. Gar. Rept. **20**:126. 1909) now makes it possible at least to place species of this genus in fairly well-marked groups. This proposed species will be somewhat aberrant in the *O. grandiflora* group. That the present species has nothing in common with the *O. biennis* group is evident not only from GATES's key, but is attested by the well-known fact that in that group the petals of all the recognized western species (*O. strigosa, O. Hookeri,* etc.) become

paler, pinkish or even white, on drying. GREENE is the only writer who has mentioned a western form (California) in which the petals remain yellow, or turn a deeper yellow, but he referred this to the misunderstood *Oenothera grandiflora* Ait., which Miss VAIL (Torreya **5**:9. 1905) has since definitely located for us. It seems strange, however, that neither HOWELL nor PIPER make any mention in their floras of the large-flowered species represented by this and the next.

MACBRIDE reports this species as scattering in the foothills but more abundant upon the adjacent mountain slopes, near Boise, Idaho; no. 262, June 18, 1910.

Onagra (OENOTHERA) **Macbrideae,** n. sp.—Annual, from a rather slender, vertical taproot: stem simple below or sometimes with one or two smaller accessory erect stems from the crown, usually sparingly branched above, 4–8 dm. high, glabrate in appearance but with a sparse crisped pubescence and a few longer ciliations: leaves glabrate or more evidently pubescent, especially on the midrib or veins which are often substrigose; the radical leaves narrowly oblanceolate, tapering above to the acute apex; cauline leaves similar but smaller and passing into the sessile bracts: inflorescence open from the first: calyx lobes nearly glabrous, about 3 cm. long, shorter than the glabrous slender tube, the linear tips short: petals yellow, thin, fading to a deeper yellow or orange red, obovate-obcordate, about 4 cm. long, twice as long as the filaments: anthers more than 1 cm. long: pistil not protruding from the bud, about equaling the petals: capsule moderately fusiform, nearly straight, and 8-costate, 2–3 cm. long: seeds apparently wing-angled.

Two such splendid plants as these by one collector, seem quite an achievement for one season. In so limited a genus, since both are from the same state, one might suspect that they should be united, but that is impossible, for one is a coarse, pubescent, spreading biennial with woody stems and crowded inflorescence: the other a glabrate, erect, herbaceous annual with few and much larger flowers.

That this species is indigenous can scarcely be doubted. It was secured more than 50 miles from a railroad in a practically uninhabited desert area in the Owyhee Mountains, Idaho. It affords me much pleasure to dedicate it to Mrs. C. M. MACBRIDE, who so industriously and discriminatingly assisted her son in the field work during most of the season of 1910. Type no. 473, Twilight Gulch, July 27, 1910.

Dodecatheon dispar, n. sp.—Glabrous throughout, obscurely, if at all, granular-glandular in the inflorescence: rootstock short, thick,

ascending or erect, producing an abundance of fleshy roots: leaves numerous, oblanceolate, tapering gradually into the long, margined base, tapering lanceolately toward the subacute apex also, 2–3 dm. long: scapes 4–6 dm. high, few-flowered (1–6), the pedicels very unequal: calyx tube obconical, about 5 mm. long; calyx lobes linear-lanceolate, longer than the tube: the sinuses broadly rounded: corolla lobes lance-linear, one-half longer than the sepals, the tube very short: stamens distinct and sessile, stout subulate, as long as the sepals: capsule circumscissile near the apex, then splitting at the summit only into 5 valves, each of which opens for a shorter distance in the dorsal suture, ovoid to oblong, equaling the calyx lobes.

Among the operculate species, having distinct anthers, I can find none with which to compare this large glabrous form.

MACBRIDE 672, moist flats near the Trinity Lakes, Elmore Co., Idaho, August 29, 1910.

COLLOMIA GRANDIFLORA **axillaris,** n. var.—Stems slender, cinerous-puberulent, 3–5 dm. high: leaves puberulent: the capitate flower clusters small and few-flowered, on very short foliar-bracted branchlets axillary in most or even all of the leaves, the terminal cluster often not much larger than the others: calyx very glandular.

Collomia grandiflora is thus seen to be exceedingly variable. Any one comparing this variety with material typical of the species would have no hesitation in declaring them remarkably distinct. But with *C. grandiflora diffusa* Mulford before you, and a goodly number of intermediates between the species and the varieties, one hesitates to name it at all. So striking a variation, however, ought to be designated in some way.

MACBRIDE 580 is the type; Trinity, Elmore Co., August 8, 1910, open hillsides. Less well represented by his no. 376, Silver City, July 14, 1910, steep hillsides.

Phlox aculeata, n. sp.—Depressed-caespitose on the intricately slender-branched caudex: stems slender, sparsely crisped, viscid-pubescent, especially above, the internodes short or nearly wanting: leaves densely crowded, filiform, straight or curved, rather rigid and aculeate, the midrib and margins slightly thickened, obscurely puberulent and the uppermost also minutely glandular; usually only 10–12 mm. long but often a few of them are a half longer: flowers solitary or more often 3–5 at the ends of the branchlets, on pedicels 3–7 mm. long: calyx densely glandular-pubescent,

apparently cleft nearly to the base: its lobes nearly linear, scarious on the slightly broadened base, acuminate and aculeate above, 7–8 mm. long: corolla usually a deep pink, shading to lighter or even white; its tube a half longer than the calyx; its lobes narrowly ovate, rounded and obscurely denticulate at summit, about 8 mm. long: style and the longer stamens as long as the corolla tube: capsule large, spreading the calyx lobes apart, 4–5 mm. long: seeds oblong-ovate, rugulose and minutely puncticulate.

It might be referred to the *P. caespitosa* group but for the usually 3–5-flowered cymes which relate it to the *Kelseyi* group (5 species), and of these it is most nearly related to *P. pinifolia* Brand., which is erect and with calyx and pedicels pilose and not glandular.

MACBRIDE tells me this is common on the dry bench lands in the vicinity of New Plymouth, in the Payette Valley. His collection, no. 73, New Plymouth, May 20, 1910, supplies the type.

Phacelia luteopurpurea, n. sp.—Slender annual, sparingly branched from the base and upward, hispidly short-hirsute, 1–2 dm. high: leaves 2–5 cm. long, somewhat irregularly bipinnate, the oblong-linear lobes rarely few-toothed: inflorescence rather densely and conspicuously dark glandular-pubescent: sepals linear, spatulate, as long as the corolla tube and exceeding the mature capsule, hispid as well as glandular: corolla narrowly campanulate; the tube yellow or yellowish, only 3–4 mm. long, more than twice as long as the broadly rounded spreading purple lobes: stamens nearly as long as the corolla tube, inserted in the margin of pocket-like depressions near the base but without any vertical folds: style 2-cleft at apex only: capsule ellipsoidal, 2 mm. or more long; the ovules about 16; the seeds often fewer, irregularly oblong, with fine transverse acute rugulae.

Most nearly related to *P. bicolor* Torr., but at once distinguished by its glandular pubescence and short corolla. These two, with *P. glandulifera* Piper, *P. Ivesiana* Torr., and *P. Fremontii*, are the members of the section EUGLYPTA Wats. (MICROGENETES A. DC.).

The type is MACBRIDE 84, New Plymouth, Idaho, May 21, 1910; sandy soil.

Madronella purpurea (Howell), n. comb.—*Monardella purpurea* Howell, Fl. N.W. Am. 550.—Low, scarcely more than 2 dm. high, the shrubby base freely branched: twigs of the season very numer-

ous, slender, simple, puberulent, 10–18 cm. high, very leafy: leaves entire, oblong or ovate-lanceolate, subacute, rather thick, obscurely puberulent or nearly glabrous, 12–25 mm. long, usually much exceeding the internodes, tapering into a short petiole: head of flowers close, 15–20 mm. high and about as broad; involucral bracts in two rows, the outer only slightly shorter, all obovate: calyx tube about 10 mm. long, minutely hirsute; the small triangular teeth softly hirsute: corolla tube minutely pubescent, distinctly exceeding the calyx, its linear purple lobes about half as long as the tube.

GREENE'S argument (Leaflets 1:168) for discarding the name *Monardella* seems convincing; therefore, I transfer two most excellent species. The above is re-characterized in the light of MACBRIDE'S perfect specimens from Silver City, in the Owyhee Mountains, no. 434, growing in granite soils.

Madronella parvifolia (Greene), n. comb.—*Monardella parvifolia* Greene, Pl. Baker. 3:22. 1901; appearing in COULTER and NELSON'S *Manual* as *Monardella parviflora*, a slip in copying.

LITHOSPERUM RUDERALE **lanceolatum,** n. comb.—*L. lanceolatum* Rydb., Mem. N.Y. Bot. Gard. 1:233. 1900.

There can be little doubt that PIPER is right (Contrib. U.S. Nat. Herb. 11:486. 1906) in replacing *L. pilosum* Nutt. by *L. ruderale* Dougl.; but not in reducing *L. lanceolatum* to complete synonomy. RYDBERG'S name probably should be retained as representing a recognizable variety. The characters on which he relied to separate it specifically from its nearest ally, *L. pilosum*, are characters of degree, mainly size. This character may so readily be accounted for by environment that one is not justified in giving more than varietal significance to it. In the light of most remarkable specimens of this variety secured by MACBRIDE at Big Willow, Canyon Co., no. 110, the salient characters may be restated as follows:

Stems very numerous, stout 4–6 dm. high: the inflorescence paniculately branched, sepals elongating and surpassing the very large nutlets, which are distinctly keeled and provided with a conspicuous flaring white polished collar bordering the broad concave basal scar.

Pentstemon Macbridei, n. sp.—Caudex woody, subterranean: stems several to many from each of the few crowns of the caudex, puberulent, slender, simple, erect, closely and equably leafy, 1–3 dm. long exclusive of the ample inflorescence: leaves puberu-

lent, narrowly linear, tapering to both ends, 3–6 cm. long, all sessile except the lowest which are somewhat reduced in size and short-petioled, the upper passing into the bracts which are gradually reduced upward: the cymose panicle ample, 1–2 dm. long, or often longer, the open, lower branchlets more or less elongated and bearing simple or compound cymes, puberulent as are also the pedicels which are often much longer than the calyx and with a small pair of bractlets: sepals broadly ovate-lanceolate, acute, green and glabrate with subscarious margin, 5–6 mm. long: corolla showy, bluish-purple, gradually dilated, moderately bilabiate, glabrous within and without, its tube 14–16 mm. long, its oval-oblong lobes spreading, about 5 mm. long: anthers saccate, opening only above the middle, glabrous even on the line of dehiscence, sterile filament flattened at apex, wholly glabrous.

This beautiful *Pentstemon* seems not to be closely related to any described species except *P. gracilenta* Gray, from which it is readily distinguished. That has glabrous herbage and is glandular pubescent in the inflorescence. Its leaves are broader and largely basal, upwardly becoming distant and reduced; the relatively smaller and narrower inflorescence is naked-pedunculate; and the corolla is smaller and the sterile filament more or less bearded.

I take pleasure in naming this for my young friend J. FRANCIS MACBRIDE, who collected so industriously during the summer of 1910. The type is no 105, secured on loamy slopes, near Big Willow, Canyon Co., Idaho, May 27.

Pentstemon perpulcher, n. sp.—Stems few–several from a short thick woody caudex, 4–8 dm. high including the inflorescence, erect or ascending, puberulent below, becoming glabrous above: basal leaves narrowly oblanceolate, 3–10 cm. long, including the tapering base and petiole; cauline linear-lanceolate, with sessile clasping base, reduced upward and passing into the linear bracts: thyrsus crowded or more open, rather narrow and secund, 1–3 dm. long: sepals glabrous, ovate, acute with subscarious and minutely erose margins: corolla blue, mostly less than 20 mm. long, with moderately dilated glabrous throat and oval lobes: anthers dehiscent, glabrous; sterile filament stiffly bearded at the tip, not at all dilated.

I hesitate to designate another species in the *P. glaber* group. Several segregates have already been published by various authors, none of which, however, seems to have anything to do with the specimens in hand. The

characters relied upon to separate the new species are (*a*) the erect slender stems with the narrow leaves and secund thyrse, giving the plant the aspect of *P. unilateralis* Rydb.; (*b*) the pronounced puberulence of the plant below the inflorescence; (*c*) the short corolla, a third shorter than any of the other species of the *P. glaber* group; (*d*) the glabrous anthers; (*e*) the habitat, the plant seemingly much at home on dry banks of the sage brush deserts of western Idaho. All of these characters are directly opposed to the accepted ones of typical *P. glaber* Pursh.

MACBRIDE 80, New Plymouth, Canyon Co., Idaho, May 21, 1910, is the type.

Pentstemon Woodsii, n. sp.—Moderately short pubescent throughout, and more or less glandular upward: stems wholly herbaceous, from the branches of a short woody subterranean caudex, erect, leafy, terminating in a small cyme of three or five flowers: leaves not at all coriaceous, oblong to oblong-lanceolate, acute, ascending, dentate or denticulate except the lower which are smaller than the others and entire, the larger 3 dm. or more in length and much longer than the internodes: sepals narrowly lanceolate, about 10 mm. long: corolla purplish blue, gradually dilated upward, about 3 cm. long, its oval-oblong lobes less than 5 cm. long, finely woolly in the throat on the lower lip: anthers dehiscent through the junction of the two cells but not explanate, finely matted-woolly; sterile filament not dilated at apex, the very tip bearing a few long woolly hairs: style slender, scarcely exserted but surpassing the included stamens.

I would refer the present specimens to *P. montanus* Greene (of which I have seen no authentic specimens) were it not that GREENE says of that "leaves cinerously puberulent, corolla pink-purple, and sterile filament naked." He would hardly have failed to mention the decidedly glandular pubescence of the inflorescence and the thin, not at all leathery, leaves. In TWEEDY'S specimens, cited as the type, it is mentioned that the corollas blacken in drying, which is not the case at all in *P. Woodsii.*

The fine specimens taken as the type were received from Mr. C. N. WOODS, Supervisor of the Sawtooth Forest Reserve, no. 265, for whom it is a pleasure to name the species.

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THE DEVELOPMENT OF THE ASCOCARP OF LACHNEA SCUTELLATA[1]

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(WITH PLATE IX AND FIFTY-ONE FIGURES)

The material upon which the present study is based was collected at Cold Spring Harbor, Long Island, where the ascocarps of *Lachnea* were found in large numbers upon decaying wood in damp places. The ascocarps appear to be frequently produced in crops, as a considerable number of about the same age are often found on a single log. If all of these are removed while still young, a second crop will usually appear in a few days. If now the young ascocarps are removed as they appear, successive crops may continue to be produced for some time. By this means a large number of young stages can be quite easily obtained.

For microscopical study, sections were cut 3–5 μ thick and stained with Flemming's triple or Haidenhain's iron-alum hematoxylin. The latter gave the best results.

Lachnea scutellata has a disk-shaped ascocarp, 2 mm.–1 cm. in diameter, the upper surface of which is covered by the hymenium, which is colored red. The margin and lower surface of the disk are brown and thickly beset with long brown setae. The setae are long, septate hyphae, the outer walls of which are greatly thickened. A cross-section of an ascocarp (plate fig. 1) shows that the inside is composed of densely interlacing hyphae, while the margin and lower surface are covered by a parenchymatous cortical layer consisting of large, thick-walled hyphae which run nearly parallel to each other and perpendicular to the outer surface of the ascocarp. WORONIN (**38**) described the ascocarp of *Lachnea scutellata* as originating in the production of an archicarp, which soon became surrounded by vegetative hyphae that obscured its further development.

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. —.

In the youngest specimens obtained, the archicarp consisted of a row of 7–9 cells, which had just become surrounded by vegetative hyphae. The ascogonium is the penultimate cell of the archicarp, which when mature consists of about 9 cells (plate fig. 3). The ascogonium and all of the vegetative cells are multinucleate. In the youngest specimens the ascogonium was about one-third to one-fourth its size at maturity. There was observed neither at this time nor later any sign of an antheridium, and since in the young specimens the ascocarp consisted of only a few hyphae, it should have been plainly visible even if degenerated. It seems probable, therefore, that no antheridium is present.

Before the ascogonium reaches its mature size, the walls of the vegetative hyphae on the outside of the young ascocarp become thickened, and these hyphae form the outer covering of the ascocarp (plate fig. 2). This covering undergoes no further growth, but remains at the base of the mature ascocarp and forms the first part of the cortex. The hyphae around the ascogonium remain active and give rise, over the ascogonium, to small hyphae which grow out to form paraphyses (plate fig. 3). The same hyphae which give rise to the hyphae producing the paraphyses give off branches, around the region of the paraphyses, some of which grow up and add to the cortex, while others grow out and form setae. As the cells of the setae and cortex reach their mature size, they become greatly vacuolated and the outer walls increase greatly in thickness. When the setae are first formed, they are bent down toward the center of the top of the young ascocarp, and thus form a covering over the developing hymenium (plate fig. 4). When a part of the cortex is once formed, the development of that part ceases, and further additions are made only in the region between the paraphyses and the cortex. The hyphae here remain active and give rise on one side to paraphyses and on the other to setae and more of the cortex of the ascocarp. As this continues, the older setae are carried outward, and finally come to be on the lower surface of the ascocarp. The setae which are formed first are not as long as those which are formed later, so that the setae around the margin of the disk are longer than those on the under surface. As the hymenium increases in diameter, by the production of more

paraphyses and the pushing in of the ascogenous hyphae, which by this time have grown out from the ascogonium, it becomes too large to be covered by the setae and is thus exposed. When this has occurred, the ascocarp has attained its mature form (plate fig. 1). The relation of the various parts of the ascocarp is shown diagrammatically in fig. 1. In this diagram are shown both the ascogonium and asci, whereas the ascogonium always disappears before the formation of asci.

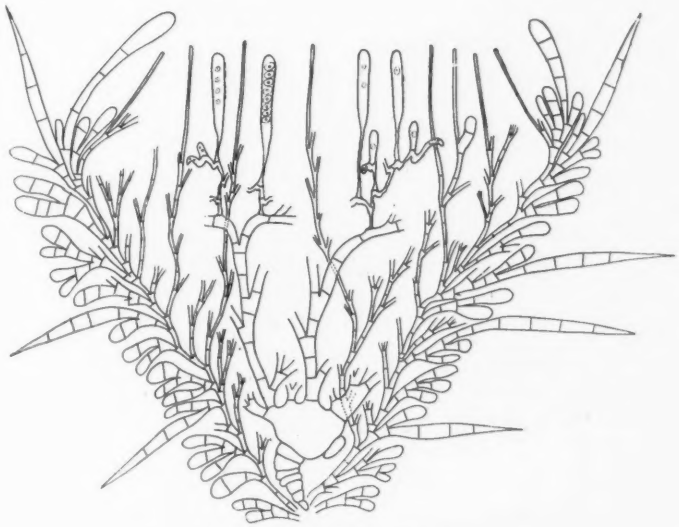
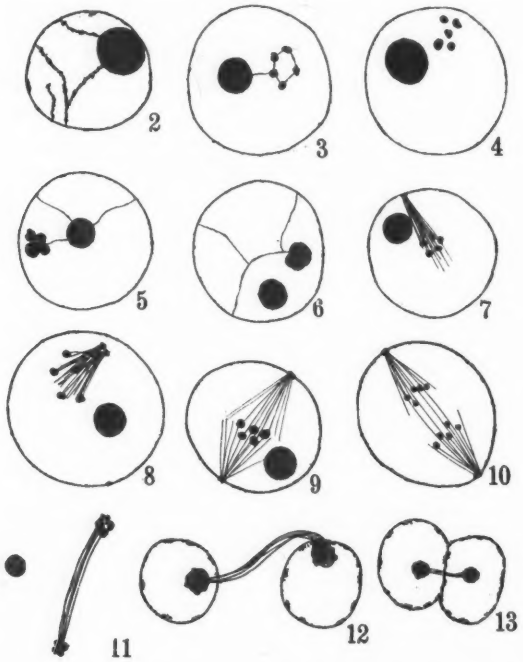


FIG. 1.—Diagrammatic cross-section of ascocarp

The vegetative nuclei usually contain a nucleolus and a small amount of scattered chromatin, but sometimes the chromatin is collected into a rounded mass resembling a nucleolus. In dividing the vegetative nuclei show five chromosomes. The nuclei of *Lachnea* contain comparatively little stainable material, as will be seen from the figures. This scarcity of stainable material makes the figures appear diagrammatic. Such is not the case, however, as all figures were drawn with a camera lucida, and in those illustrating nuclear details, all of the stainable material in the nuclei is

figured. In most cases the cytoplasm is omitted, as this resembles that usually found in Ascomycetes.

The nuclei in the ascogonium resemble the vegetative nuclei



FIGS. 2–13.—Fig. 2, nucleus of ascogonium in resting stage; fig. 3, formation of chromosomes in nucleus of ascogonium; figs. 4–6, arrangement of chromosomes when first found in nucleus of ascogonium; fig. 7, formation of spindle in nucleus of ascogonium; fig. 8, division of centrosome in nucleus of ascogonium; the centrosomes are on the nuclear wall, but owing to their position appear to be inside the nucleus; fig. 9, metaphase in nucleus of ascogonium; fig. 10, anaphase in nucleus of ascogonium; fig. 11, telophase in nucleus of ascogonium; fig. 12, reorganization of nuclei in ascogonium; fig. 13, reorganization of nuclei, in contact, in ascogonium; all ×11,200.

except that they are somewhat larger. The chromatin is usually scattered throughout the nucleus, but sometimes it is arranged in a definite spireme (fig. 2). This condition probably indicates the approach of division. It has not been possible to determine defi-

nitely whether or not the spireme is continuous. Often several loops are tangled together, so that it is impossible to follow individual parts. Still more frequently parts of the spireme run along the nuclear membrane for considerable distances, so that even if it were continuous it could be followed only with considerable difficulty. At other times there appear to be definite breaks. This appearance may be due to a failure of the spireme to take the stain or to poor fixation, but there is nothing to indicate that such is the case. The spireme, soon after its formation, appears to contract and divide to form five chromosomes (figs. 3, 4). The chromosomes may be rather widely separated (fig. 4), but frequently they are collected together into a compact group resembling a second nucleolus (figs. 5, 6). The group can be distinguished, however, from a nucleolus by its irregular outlines. This grouping of the chromosomes is not confined to the ascogonium, but can be seen throughout the ascogenous hyphae and in the prophases of the second and third divisions of the ascus. It is probably also the explanation of the grouping of the chromatin seen in the vegetative nuclei.

While the chromosomes are being formed, linin fibers make their appearance in the nucleus. At the same time a centrosome appears on the nuclear membrane. This was not visible during the resting condition and appears to arise *de novo*. The centrosome is not a point, but rather a flattened area, apparently composed of many granules. When the centrosome was first observed, it was already connected with the chromosomes by the linin fibers in the nuclear cavity (fig. 7). Soon after this the centrosome (fig. 8) divides, and the daughter centrosomes move apart and come to be situated at the opposite poles of the complete spindle (fig. 9). The centrosomes in fig. 8 are against the nuclear membrane, but owing to their position appear in the figure to be within the nucleus. The five chromosomes then divide and five daughter chromosomes proceed to each of the opposite poles (fig. 10). The nuclear membrane now breaks down, and the two groups of chromosomes and the nucleolus, which soon disappears, are left free in the cytoplasm (fig. 11). The two groups of chromosomes are usually separated far enough so that when they reorganize the daughter nuclei are separated by an appreciable distance (fig. 12). Frequently, how-

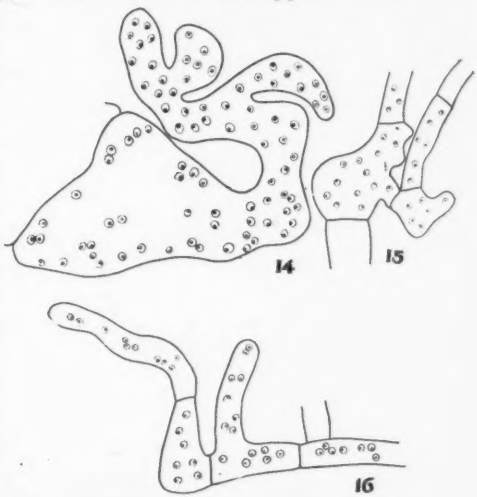
ever, the daughter nuclei reorganize so close together that after a slight growth they are pressed against each other and resemble fusing nuclei (fig. 13). The spindle fibers are frequently present at this stage, and can be seen connecting the two masses of chromatin, which are still visible in the daughter nuclei. Frequently the masses of chromatin lie against the nuclear membrane, and the disappearing fibers are entirely outside the nucleus, but at other times the fibers appear to cross the nuclear cavity, as in fig. 13. Frequently the chromatin appears, at first sight, to be in the center of the nucleus, when in reality it is lying against the membrane. This is due, of course, to the fact that the chromatin is at the upper or lower surface of the nucleus as it is viewed from above.

Division seems to take place rapidly throughout the growth of the ascogonium and the development of the ascogenous hyphae. The nuclei do not divide simultaneously, as all stages, including resting nuclei, can be found in a single ascogonium. There appear, however, to be periods in which division takes place, followed by others in which all of the nuclei are in the resting condition, for a large number of divisions are frequently found in a single ascogonium, while others show only resting nuclei. The same type of division that has just been described and the same number of chromosomes persist throughout the development of the ascogonium and ascogenous hyphae. The nuclei decrease somewhat in size during the growth of the ascogonium, and in the early stages of the development of the ascogenous hyphae, but as the ascogenous hyphae develop further, the nuclei increase in size until they come to be slightly larger than in the young ascogonium.

No fusion of nuclei has been observed in the ascogonium or in the ascogenous hyphae except in the tips where two nuclei fuse to form the primary nucleus of the ascus. A number of cases were seen in which two nuclei were pressed against each other, but in all of these the nuclear membrane was intact between the nuclei, and the appearance seemed to be due to the fact that the nuclei, after division, had reorganized close together, in the manner previously described. It may be said that a fusion of the nuclei would be hard to find, but they have been looked for very carefully in a large number of well fixed and stained preparations. The slight

decrease in the size of the nuclei during the development of the ascocarp and the persistence of the same number of chromosomes throughout the ascogonium and ascogenous hyphae, moreover, indicate very strongly that a fusion of nuclei during this stage is not to be expected.

When the ascogonium has reached its mature size, it gives off a number of large ascogenous hyphae which are multinucleate from the first (plate fig. 3). The nuclei do not appear to be arranged in pairs or in any other definite manner, but to be scattered irregularly in the hyphae (fig. 14). They are undergoing division rather rapidly, as has been previously described. About this time the cytoplasm and nuclei of the other cells of the archicarp begin to degenerate. These cells apparently do not fuse together as in *Ascophanus carneus* (CUTTING 7). The ascogenous hyphae grow up among the vegetative hyphae which are situated over the ascogonium and have been mentioned as giving rise to paraphyses.



FIGS. 14–16.—Fig. 14, outgrowth of ascogenous hyphae from ascogonium; fig. 15, storage cells giving off paraphyses; fig. 16, tips of ascogenous hyphae in hymenium; all ×525.

As the ascogenous hyphae increase in length, they branch freely and become divided up into a number of large multinucleate cells. Some nuclei are left in the ascogonium and these finally degenerate. When the ascogenous hyphae are growing out from the ascogonium, the vegetative cells over the ascogonium (plate fig. 3) are slender, densely protoplasmic, and extend upward toward the covering of the ascocarp. They thus have the appearance of young paraphyses, but do not take part in the formation of the hymenium until they have developed further. As they grow up they branch freely and

become thicker and less densely protoplasmic. As the developing ascogenous hyphae grow up and branch among these vegetative hyphae, the older parts of the vegetative hyphae cease to have the appearance of paraphyses, while the younger parts still form a layer ahead of the ascogenous hyphae. When the place where the hymenium is to be formed is finally reached, the layer of paraphyses is thus already completely developed (plate fig. 4). The continued upward growth and branching of the vegetative and ascogenous hyphae causes the hymenium to have a much greater diameter than it would have had if it had been formed before the branching had taken place. Some of the vegetative hyphae in the subhymenial layer give off branches which form large, densely staining storage cells. These in turn give rise to more paraphyses (fig. 15). In a few cases nuclei in these storage cells have been seen to be fusing, and since in some cases the fusing nuclei are exceptionally large, it may be that nuclei which have been formed by fusion may themselves fuse. The fusion of nuclei in the storage cells is of regular occurrence in *Leotia* (BROWN **6**), but is probably exceptional in *Lachnea scutellata*, as most of the nuclei in the storage cells of this species are small and of nearly uniform size.

While the storage cells are being formed in the subhymenial layer, the ascogenous hyphae can be seen, in the same region, as rows of large multinucleate cells. These give off smaller multinucleate branches which extend upward into the lower part of the hymenium (fig. 16). It is from these branches that the asci are to be formed. The tips of these branches frequently contain two nuclei, and it seems probable that these are cut off together in a single cell, as no such uninucleate cells have been observed in the hymenium or subhymenial layer, although binucleate cells are of frequent occurrence. It is, of course, still possible that uninucleate cells may sometimes be cut off, and that these may have been overlooked, as the uninucleate condition would probably last only a short time. The cutting off of two nuclei in the tip of an ascogenous hypha has been described by MCCUBBIN (**28**) in *Helvella elastica*. The cutting off of two nuclei or a single one, which subsequently divided, in *Lachnea scutellata* would probably not have any effect on the further development, since, as has already been

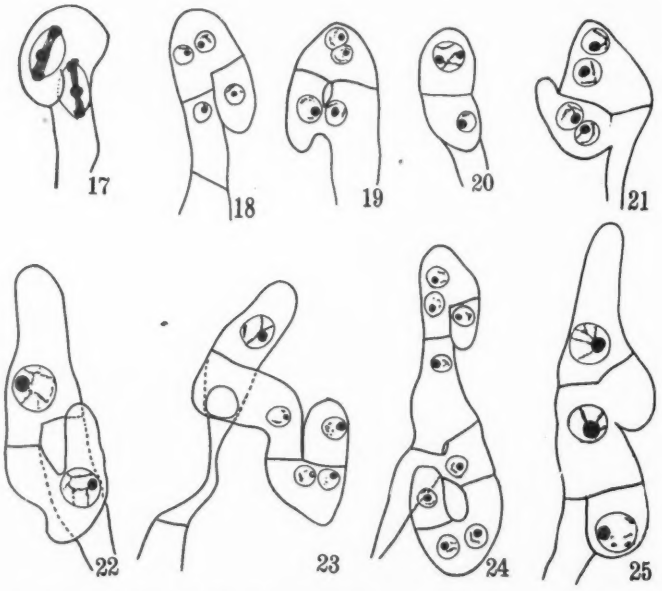
described, the nuclei undergo division in the ascogenous hyphae, so that the two nuclei which are in the tip of a hypha are probably closely related. There appears, moreover, as has been previously pointed out (BROWN **6**), to be no reason for thinking that the relation of fusing nuclei can make any difference, if these are all in the same plant and are derived from a single nucleus, with the haploid number of chromosomes.

The nuclei in those cells of the ascogenous hyphae which are below the hymenium finally degenerate. In doing so they often swell up to several times their original size, after which the nuclear membrane gradually disappears. This process is quite similar to that described by HARPER (**22**) for the nuclei in the trichogyne of *Pyronema confluens*. Before degenerating two or three of the nuclei sometimes fuse together. Such fusions are not confined to the nuclei of the ascogenous hyphae, but may occur in other degenerating cells.

The binucleate cells previously described as being formed from the ascogenous hyphae grow up in the hymenium and bend over at the tip. The two nuclei pass into the bent portion and divide in the same manner that has been described for the nuclei in the ascogonium (fig. 17). At metaphase there are five chromosomes, and at anaphase five pass to each pole. Walls come in between the daughter nuclei of each pair, thus forming a binucleate penultimate and a uninucleate ultimate and antipenultimate cell (fig. 18). This is of course a typical hook. The two nuclei in the penultimate cell may fuse to form the nucleus of an ascus (fig. 20), but often they divide and give rise to the nuclei of another hook (fig. 24). The ultimate cell usually grows down and fuses with the stalk (fig. 19), after which the nucleus from the stalk usually migrates into the ultimate cell (fig. 21), although occasionally the nucleus of the ultimate cell may pass into the stalk. After the nucleus of the stalk has migrated into the ultimate cell, it may fuse with the nucleus of the ultimate cell to form the primary nucleus of an ascus (fig. 22), but usually the two nuclei divide and the ultimate cell grows out to form another hook (figs. 23, 24). Sometimes the nucleus formed by the fusion of the nuclei of the ultimate and antepenultimate cells does not develop further. This is usually asso-

ciated with a vacuolated condition of the cytoplasm. Fig. 25 shows a case in which the penultimate cell has developed into a second hook. The nuclei of the ultimate and antepenultimate cells have fused, but the fusion nucleus has not developed further. The penultimate cell of the second hook has given rise to an ascus, while the nucleus of the ultimate cell has migrated into the antepenultimate and fused with its nucleus.

The processes described above, by which either the ultimate



FIGS. 17–25.—Fig. 17, tip of ascogenous hyphae, showing form of hook and division of nuclei; fig. 18, binucleate penultimate and uninucleate ultimate and antepenultimate cells; fig. 19, fusion of nuclei in penultimate cell and fusion of ultimate and antepenultimate cells; fig. 20, fusion nucleus in antepenultimate cell; fig. 21, migration of nucleus from antepenultimate to ultimate cell, followed by outgrowth of ultimate cell; fig. 22, formation of asci from both ultimate and antepenultimate cells; fig. 23, formation of hook from ultimate cell and ascus from penultimate; fig. 24, formation of hooks from both ultimate and penultimate cells; fig. 25, case in which nucleus from antepenultimate cell migrated into ultimate and fused with nucleus of ultimate; a hook was formed from binucleate penultimate cell, the penultimate cell of which in turn gave rise to an ascus, while the nucleus of the ultimate cell migrated into the antepenultimate and fused with its nucleus; all ×1400.

or antepenultimate cell may give rise to a hook, may be repeated many times, so that a large number of asci may be formed finally from a single hypha. Even in young ascocarps, five or six hooks may frequently be seen joined together in various ways, and if it were possible to follow a hypha for a considerable distance, the above number would of course be greatly increased.

The significance of these phenomena has been discussed in a previous paper on *Leotia* and *Geoglossum* (BROWN **6**), in which genera they also occur.

As new hooks are successively developed from older ones, that part of the ascogenous hypha which connects the successive hooks, as well as the older parts of the hypha, become vacuolated to such an extent that no cytoplasm can be seen in them. Despite this fact, new hooks and asci are formed quite rapidly. It seems probable, therefore, as HARPER (**22**) suggests, that the developing asci obtain their nutrient material from the paraphyses, which are in contact with them, by transfusion through the walls.

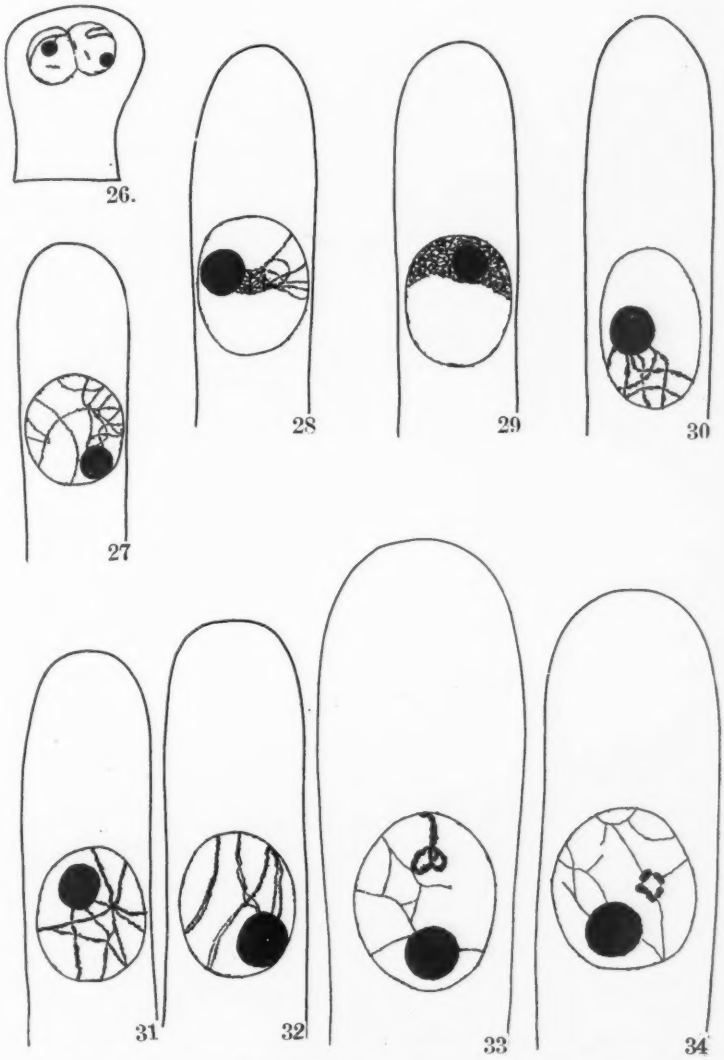
The multiplication of the number of hooks gradually raises the level at which asci are formed. At the same time, the level at which the paraphyses come off is also raised by the formation of new ones from the basal portion of older ones and from storage cells which are being continually formed at a higher level. As growth continues and the hymenium rises higher and higher, the subhymenial layer is increased in height by the addition of the older parts of the hymenium, which are gradually left behind.

While the hymenium is thus being raised, it also increases in diameter. As has already been described, the cells between the hymenium and cortex continually produce new cells which give rise to paraphyses around the margin of the hymenium. At the same time, hooks formed from the ultimate or penultimate cells of older ones grow in among the paraphyses. Owing to the processes described above, an ascocarp, after it assumes its mature form, may increase greatly in both height and diameter.

When the two nuclei which fuse to form the primary nucleus of the ascus are in the process of fusion, they contain comparatively little chromatin. This is scattered somewhat irregularly on linin fibers, but shows an approach to the spireme condition

(fig. 26). The fusion nucleus grows rather rapidly, and as this continues the chromatin soon comes to be arranged in a definite, fine spireme (fig. 27). When this condition has been reached, the spireme does not usually show any free ends, and it can frequently be traced as a continuous thread for considerable distances. It is impossible, however, to follow it through some of the tangles. Frequently threads run to the nuclear membrane or nucleolus, after which it is not possible to trace them further. This suggests that the spireme is not continuous throughout its entire length, but this conclusion must be considered doubtful, as it is difficult to follow a spireme along the nuclear membrane, which is usually irregularly thickened, or to distinguish it from the nucleolus when it is in contact with the latter. While the nucleus is still far from its final size, the spireme shows the approach of synizesis by beginning to collect in a tangle either around or to one side of the nucleolus (fig. 27). This usually continues until all of the spireme is arranged in a dense tangle in which little detail can be seen (fig. 29). No evidence of a fusion of spiremes during this stage was observed. An examination of figs. 27 and 28 will show that the spireme is not double as it goes into synizesis. The spireme was occasionally seen contracted into a mass about as dense as the nucleolus. This extreme condition may have been due to fixation, but the regular occurrence of synizesis at this stage, and in material in which the fixation seemed to be perfect, certainly seems to indicate that synizesis is, as MOTTIER (**29**) thinks, a stage in development, and not an artifact due to fixation, as is claimed by SCHAFFNER (**32**). This view is supported by the fact that the spireme is quite different in appearance before and after synizesis. Synizesis probably lasts for a considerable time, as the nucleus and ascus grow considerably during this period.

At the end of synizesis the spireme, which is now much thicker than before, loosens up and becomes spread through the nucleus (figs. 30 and 31). The continuity of the spireme throughout its length at this stage is, just as before synizesis, doubtful. After the spireme has become spread through the nucleus, it splits longitudinally (fig. 32). This splitting appears to extend through almost if not quite the entire length of the spireme. The two halves,



FIGS. 26–34.—Fig. 26, fusion of two nuclei in ascus; fig. 27, early stage in approach of synizesis in nucleus of ascus; fig. 28, later stage in approach of synizesis; fig. 29, synizesis in nucleus of ascus; fig. 30, spireme just after synizesis; fig. 31, spireme spread through nucleus; fig. 32, split spireme; fig. 33, contracted spireme just before formation of chromosomes; linin fibers apparent; fig. 34, nucleus with five chromosomes and well developed fibers; all ×2800.

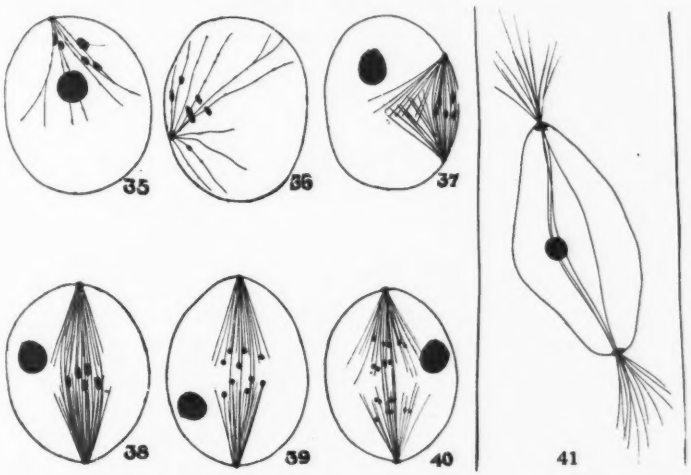
however, soon come together again, after which all traces of the split are usually lost, although sometimes evidences of it may be apparent even after the formation of the chromosomes.

After the two halves of the spireme have come together, it begins to contract. This contraction continues until the spireme shortens very considerably (fig. 33). The spireme at this stage has the appearance of a continuous thread, the ends of which are probably free. The spireme finally segments into five somewhat elongated chromosomes (fig. 34). Each of these chromosomes is probably bivalent, since the nucleus received five chromosomes from each of the two nuclei which by fusing gave rise to it. The bivalent condition, however, is not indicated by the form of the chromosomes. In this they are probably similar to those of most plants. In *Peperomia* (BROWN **4**), however, the two halves appear during the heterotypic prophase, as separate chromosomes connected by linin fibers; while in *Oenothera* (GATES **17**) the diploid number of chromosomes appears at the same stage, and in this case some of the chromosomes may not be arranged in pairs.

As the spireme contracts, linin fibers appear within the nucleus (fig. 33). Along those fibers, and especially in the early stages, there are small granules which have the appearance of chromatin. They usually stain less densely than the chromatin of the spireme, but frequently they are large and numerous enough to make the fibers along which they are scattered resemble the spireme. It was not possible to tell whether the substance of these granules passed to the chromosomes or took part in the formation of more linin fibers, but since as they disappear the number of linin fibers increases considerably, it seems probable that part of the granules take part in the formation of the fibers. No evidence of the formation of these fibers from the linin of the spireme by the migration of the chromatin has been observed, but since the continuity of the spireme in the early stages is doubtful, and these fibers may resemble the spireme very closely, such a possibility, while not probable, can hardly be said to be excluded. It is certain, however, that most of these fibers which will later on take part in the formation of the spindle are formed *de novo*.

As the spindle fibers increase in number, they become connected

with a centrosome which makes its appearance on the nuclear membrane, and some of them connect the centrosome with the chromosomes (fig. 35). No signs of this centrosome have been visible up to this time, and as there is nothing to indicate that it persists through the resting stages, it is probable that it is formed *de novo* at each division. In this respect it resembles the centrosphere-like bodies in *Polysiphonia violacea* (YAMANOUCHI **39**), the centrospheres in *Corallina* (DAVIS **11**), and the kinoplasmic caps



FIGS. 35–41.—Fig. 35, fibers attached to centrosome; fig. 36, nucleus showing extra body which appears much like a chromosome; fig. 37, late prophase of first division in ascus; fig. 38, metaphase of first division; fig. 39, early anaphase of first division; fig. 40, late anaphase, showing division of daughter chromosomes; fig. 41 telophase of first division; all ×2800.

in *Griffithsia bornetiana* (LEWIS **25**). Deeply staining granules are frequently present in the cytoplasm of *Lachnea*. These are particularly abundant around the nucleus at this division. The nuclear membrane does not have an even appearance, but is irregularly thick, and often the granules just described are in contact with it. Owing to these facts it has not been possible to trace the origin of the centrosome. The centrosome here, as in the divisions previously described, is not a spherical body, but a flattened structure composed of a number of granules.

When the five chromosomes have become connected with the centrosome, other deeply staining bodies are frequently present on the linin fibers. These are usually small and are probably similar to the granules previously described. Sometimes, however, they are as large as or larger than the chromosomes, and may bear such a striking likeness to them that there may appear to be as many as six or seven chromosomes (fig. 36). When the spindle is completely formed, these bodies may still be present on fibers connected with the spindle or nucleolus. Only very small ones, however, have been seen on the spindle, so that when the spindle is formed these bodies, which usually stain lighter than the chromosomes, can be readily distinguished from them.

After the linin fibers have become connected with the centrosome, they increase in number. The centrosome then divides, and the two daughter centrosomes take positions at the opposite ends of the spindle (figs. 37 and 38). When the spindle is first formed, it may be at any angle to the longitudinal axis of the ascus, but as division proceeds, it takes a position which is approximately parallel to it. While this is taking place, a set of fibers makes its appearance outside the nucleus. These fibers radiate from the centrosome into the cytoplasm for a considerable distance.

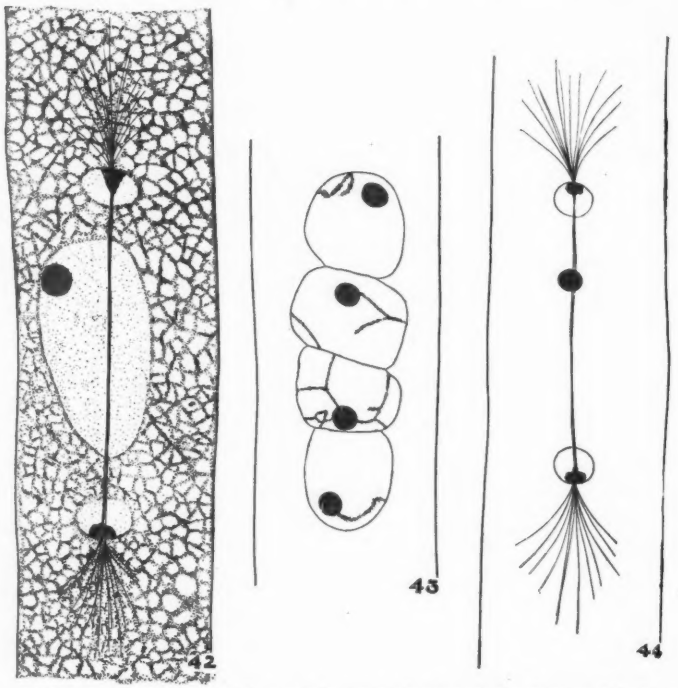
At metaphase five chromosomes are present on the spindle (fig. 38). Usually all of these appear to be somewhat elongated and have their longitudinal axis parallel to that of the spindle. Each of the five chromosomes divides transversely, but the divisions do not all take place at the same time, so that as division proceeds, anywhere from six to ten chromosomes may be counted on the spindle. Remembering that when the spireme segmented it gave rise to five elongated chromosomes which were probably bivalent, it would seem that this division probably separates chromosomes which were placed end to end on the spireme and can have nothing to do with the longitudinal split seen in the prophase. There appears to be nothing to indicate that the chromosomes which went into the fusion nucleus have persisted unchanged through the resting nucleus and the prophases of this division, and are the same as the chromosomes which are separated at metaphase. On the contrary, there would seem to have been every chance for an

exchange of material during synizesis, if not during the resting stage. The independence of unit characters in heredity would seem to favor the view that there may be an exchange of material between chromosomes, for if a given set of unit characters were permanently associated with the same chromosomes, we would expect to find different characters correlated much oftener than they are. If, however, as is generally assumed, the chromosomes are the part of an organism which is responsible for the transmission of hereditary characters, and if different chromosomes are not alike but responsible for different characters, it would be impossible for a promiscuous exchange of material between various chromosomes to occur without producing chaos. It would seem more likely that the chromosomes are so constituted that only certain kinds of material can be fitted into them, so that while chromosomes derived from different nuclei may exchange material which is responsible for similar sets of characters, they cannot exchange material which is responsible for one kind of character for that responsible for a different kind.

The chromosomes at the first division in *Lachnea* appear to approach the poles rather slowly, as anaphase is very abundant in sections. The ten chromosomes, formed by the division of the five seen at metaphase, are at first grouped at the equator of the spindle and give this stage a striking resemblance to metaphase. Finally, however, they separate into two groups of five, one of which goes to each pole (fig. 39). As the chromosomes approach the poles all of them may again divide (fig. 40). The two halves of a chromosome do not appear to be connected, but when division has just taken place the halves appear to be arranged in pairs, the constituents of which usually lie side by side on the spindle. It would seem from this that this division is due to a longitudinal splitting, and this may be connected with the splitting of the spireme seen in the prophase. A division of the daughter chromosomes as they approach the poles has been described in *Gallactinia succosa* by MAIRE (**27**) and GUILLIERMOND (**18**).

After the chromosomes have reached the poles, the fibers which connect the centrosomes continue to elongate until they become markedly bent. At the same time, breaks are formed on the

nucleus at each pole (fig. 41). Finally the groups of chromosomes break through the nuclear membrane, after which the fibers which connect the chromosomes straighten out and the groups of chromosomes are carried far beyond the limits of the nucleus (fig. 42). The nuclear membrane then breaks down. The nucleolus is left

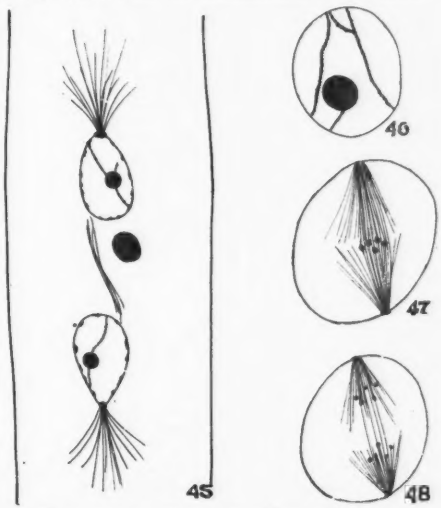


FIGS. 42–44.—Fig. 42, early stage in reorganization of daughter nuclei; fig. 43, four nuclei of an ascus in contact; fig. 44, late stage in reorganization of daughter nuclei after first division; all ×2800.

in the cytoplasm and finally disappears. Both the fibers which connect the centrosomes and those which radiate out into the cytoplasm frequently persist until after nuclear membranes have been formed around the daughter nuclei (fig. 45). Sometimes the groups of chromosomes are not separated so far, and in this case the daughter nuclei may reorganize in contact with each other.

Occasionally this may occur at both the first and second divisions (fig. 43).

When the two groups of chromosomes have reached the place where the daughter nuclei are to be reorganized, they lie at the ends of the fibers which connect the centrosomes and just below those which radiate out into the cytoplasm. A clear area then makes its appearance on the side of the chromosomes which is away from the radiating fibers (fig. 42), and a membrane is formed around this clear area (fig. 44). The centrosome appears to be on the nuclear membrane and can be distinguished until the nucleus grows considerably, but after a time it seems to disappear. When the nucleus is first formed, the chromosomes are still arranged in a group on that side of the nucleus which is near the radiating fibers. As growth proceeds this group gradually grows smaller, while masses of chromatin make their appearance on other parts of the nuclear membrane. The nuclei are usually pear shaped (fig. 45). This appearance suggests that the radiating fibers exert a pull on the nucleus.

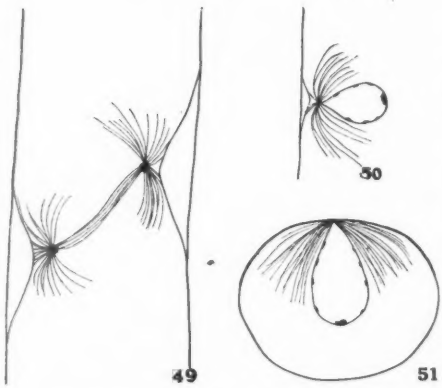


FIGS. 45–48.—Fig. 45, daughter nuclei reorganized; fig. 46, resting nucleus between first and second divisions; fig. 47, metaphase of second division; fig. 48, anaphase of second division; all ×2800.

The next division is homotypic, and shows no new features. The chromatin becomes arranged in a spireme (fig. 46) which gives rise to five chromosomes. These chromosomes are usually rather close together, and frequently they become aggregated in a rather dense mass. This phenomenon appears to be similar to the grouping of the chromosomes in the prophases of the divisions in

the ascogonium and ascogenous hyphae. The spindles of this division are similar to those of the first, and usually lie in a plane which is approximately parallel to the axis of the ascus, but, as HARPER (**21**) has shown, they may vary markedly from this position. At metaphase the five chromosomes divide and five pass to each pole. Telophase and the reorganization of the daughter nuclei appear to be entirely similar to the same processes as described at the end of the first division.

The third division is essentially like the second, except that the spindles are usually approximately at right angles to the axis of the ascus although, as HARPER (**21**) has shown, one of them may be parallel to the ascus wall. At telophase, when the masses of chromosomes have broken through the nuclear membrane, some of the fibers which radiate from the centrosome out into the cytoplasm appear to be connected to the plasma membrane around the ascus (fig. 49). Where this occurs, the plasma membrane is pulled in toward the groups of chromosomes as though the fibers which connect the groups of chromosomes with the plasma membrane, by contracting, were drawing the membrane and group of chromosomes together (fig. 49). As the groups of chromosomes approach the periphery of the ascus, the radiating fibers come to be bent backward; this may be due to the movement of the centrosomes. The nuclei reorganize in a manner similar to that described for the daughter nuclei at the end of the first division, except that a more pronounced beak is formed on the nucleus where the radiating fibers



FIGS. 49–51.—Telophase of third division; radiating fibers attached to plasma membrane; fig. 50, nucleus reorganized after third division; fig. 51, spore showing beginning of secondary thickening of wall; fibers still apparent; all ×2800.

are joined to the centrosomes (fig. 50). The plasma membrane around the ascus, which was pulled in where the radiating fibers were connected with it, has by this time very nearly resumed its normal position against the ascus wall (fig. 50). The nucleus which is still connected by fibers to the membrane is, by this means, drawn toward the periphery, and this may account for the beak and also for the further bending back which has taken place in the radiating fibers which were not connected with the membrane.

Since the fibers seem to exert a pull on both the plasma membrane and the nucleus, and to be bent as a result of the movement of the nucleus, it would seem that they must be relatively solid structures. This view is strengthened by their behavior during telophase in all three divisions. After the chromosomes have reached the poles, the fibers connecting the centrosomes continue to grow and become bent as though under tension. At the same time beaks are formed on the nuclei at both poles. This may be due to the pressure of the connecting fibers, or in part at least to a pull exerted by the fibers radiating into the cytoplasm, as in the case of the beaks formed on the eight nuclei.

HARPER (**19, 21, 22, 23**) has described the cutting out of the spores in *Erysiphe*, *Lachnea scutellata*, *Pyronema*, and *Phyllactinia*. According to this author, the fibers radiating into the cytoplasm fold back and fuse into a membrane which grows back until its edges meet at a point opposite the centrosome. FAULL (**12**) has studied spore formation in a number of Ascomycetes, and concludes that the spores are not cut out by a membrane formed of fused astral rays. According to him the spores are delimited by a limiting layer of protoplasm. On the site of this there is formed a plasma membrane about the spore, and another opposed to it lining the cavity in the epiplasm. The formation of these is probably preceded by a cleavage of the limiting layer. The exospore is formed between the two opposed plasma membranes. OVERTON (**31**) in *Thecotheus pelletieri* and FRASER (**14**) in *Humaria rutilans* describe the spores as delimited by the astral rays. In *Lachnea*, the first sign of the cutting out of the spore is the appearance of a delicate membrane at the outer limits of the recurved astral rays. This usually appears first around the centrosome

and then is formed progressively until it cuts out the spore. This membrane is apparently not formed by a fusion of the astral rays, for although it appears at their outer limit, after it is completely formed the rays are still present within the spore and are apparently as numerous as ever, and in shrunken material both the centrosome and astral rays may be drawn completely away from the spore membrane. Moreover, in *Lachnea* there do not appear to be enough fibers to fuse together to form a membrane, unless, as pointed out by FAULL (**12**), they become flattened out very considerably, and there is no evidence that such is the case. Where there are a large number of fibers, as in *Phyllactinia* (HARPER **23**), the fusion would be a much simpler matter, but that they are very numerous where the membrane appears, and disappear as it is formed, is not sufficient evidence that they fuse. It would be necessary to see the actual fusion to prove that the spore is cut out by a membrane formed of fused fibers. What part, if any, the centrosome and fibers take in the formation of the membrane is doubtful. The appearance of the membrane just outside of them suggests that they may have something to do with its position. On the other hand, sometimes even before the membrane is completely formed the centrosome may be within it and not in contact with it. Stages showing a spore partly cut out are relatively rare, which indicates that when the process is once begun it takes place rapidly. Miss FRASER (**14**) says that FAULL'S account of the cutting out of the spores "does not seem to satisfactorily explain either the persistence of the astral rays or the formation of the nuclear beak." In this connection it may be noted that in *Lachnea* the astral rays usually persist after both the first and second division, until the daughter nuclei are completely reorganized, and that beaks are frequently formed on the nuclei, although these are not so prominent as those on the nuclei of the spores.

During the early stages of the formation of the membrane, it appears to be simply a differentiated part of the cytoplasm, and it is difficult to determine exactly when a distinct wall is formed, but the wall appears to be produced on the site of the original membrane. After the wall has been formed around the spore, it begins to thicken (fig. 51). This process frequently commences in the

region around the centrosome, but it may begin at any point. After the wall has become thickened, it is easy to determine that it is a distinct wall, with plasma membranes on both sides of it. This is shown especially clearly in material which has been shrunken, when it is possible to find, side by side, cases in which all of the contents have a normal position, and others in which either the plasma membrane around the spore or the one lining the epiplasm is drawn away from the wall. At this stage the astral rays are still plainly visible.

The stage at which the nucleus retracts its beak and rounds up is somewhat variable, but it usually does not take place until after the formation of the wall. When the beak is withdrawn, the centrosome may be left in the cytoplasm, but more frequently it remains in contact with the nuclear membrane. In either case it finally disappears.

As the spore reaches its mature size the wall around it thickens and becomes the exospore.

Discussion

HETEROTYPIC MITOSIS

The method of reduction in the number of chromosomes in *Lachnea* is quite similar to that described in *Dictyota* (WILLIAMS **37**), *Fucus* (YAMANOUCHI **41**), and in a large number of the higher plants. The chromosomes are arranged end to end in the prophase of the heterotypic division, and there is no evidence of a parallel fusion of spiremes.

The reducing divisions in *Lachnea* are quite unlike those in *Phyllactinia* (HARPER **23**). This is perhaps not surprising in view of the great dissimilarity which, according to the work of DAVIS (**11**), YAMANOUCHI (**39**), and LEWIS (**25**), is shown by different genera of the Rhodophyceae. The great difference between the mitoses in *Lachnea* and *Phyllactinia* would certainly make it unsafe to carry any conclusions in regard to nuclear phenomena from one form to the other.

There is in *Lachnea* nothing resembling the double reduction described in some other Pezizineae by FRASER (**14**), FRASER and

WELLSFORD (15), and FRASER and BROOKS (16). This is in harmony with the view that there is no fusion in the ascogonium.

SEXUALITY

It is unnecessary to review here the history of our knowledge of the sexuality of the Ascomycetes, as this has been thoroughly done quite recently by HARPER (22, 23), OVERTON (31), and LOTSY (26); while the latest literature has been discussed by FRASER (16). The passage of the nuclei from the antheridium into the ascogonium of *Pyronema confluens*, as reported by HARPER (22) and confirmed by CLAUSSEN (8), would seem to have established the view that the antheridium and ascogonium are to be regarded as sexual organs, even though the antheridium may be functionless or lacking in other cases. DANGEARD'S (10) failure to find a passage of nuclei from the antheridium into the ascogonium of *Pyronema confluens* may be due, as BLACKMAN and FRASER (3) suggest, to his having worked on a different form from that observed by HARPER and CLAUSSEN. The writer has found that the antheridia may behave differently in different strains of *Pyronema confluens*. In one (BROWN 5), the antheridia never fused with the trichogyne, while in a strain of *Pyronema* (*confluens*) *omphalodes*, obtained through the kindness of Dr. F. J. SEAVER, the antheridium at the proper stage, as has been figured by him (SEAVER 34), can be readily seen fused to the trichogyne. The two strains, moreover, show differences in the conditions under which they can be grown. It is interesting in this connection that VAN TIEGHEM (35) has shown that under cultural conditions the antheridium of *Pyronema confluens* may be normal, rudimentary, or absent, while the ascogonium develops normally.

Since recent work has shown that the fusion of nuclei is the essential part of fertilization, the discussion of the sexuality of the Ascomycetes has naturally centered around the nuclear fusions. In the simple forms *Eremascus fertilis*, *Endomyces magnusii* (GUILLIERMOND 18), and *Dipodascus albidus* (JUEL 24), the antheridium and oogonium fuse and give rise at once to a single ascus. In *Eremascus fertilis* the antheridium and oogonium are uninucleate, and in all three cases the primary nucleus of the

ascus is formed by the fusion of a nucleus from the oogonium and one from the antheridium.

Among the Erysibaceae, HARPER (**19, 20, 23**) has described the fusion of a uninucleate antheridium and oogonium in *Sphaerotheca humuli*, *Erysiphe communis*, and *Phyllactinia corylea*. According to HARPER, the male and female nuclei fuse in the oogonium, and this is followed later by a second nuclear fusion in the ascus. DANGEARD (**9, 10**) has studied the development of *Sphaerotheca humuli* and *Erysiphe*, and denies the presence of a fusion in the oogonium.

BARKER (**2**) has described the fusion of an antheridium and oogonium in *Monascus*. He did not find a fusion of nuclei in the oogonium, but attributed this to his failure to get the proper stages. SCHIKORRA (**33**) has also described the fusion of an antheridium and oogonium in *Monascus*, but does not find any fusion of nuclei except the one in the ascus.

Among the Pezizineae the fusion of nuclei in pairs in the ascogonium has been described in *Pyronema confluens* (HARPER **22**), *Humaria granulata* (BLACKMAN and FRASER **3**), *Lachnea stercorea* (FRASER **13**), *Ascobolus furfuraceus* (WELLSFORD **36**), *Ascophanus carneus* (CUTTING **7**), and in the vegetative hyphae in *Humaria rutilans* (FRASER **14**). In all of the above cases a second fusion is described in the ascus. CLAUSSEN (**8**), however, after studying *Pyronema confluens*, has concluded that there was no fusion of nuclei in the ascogonium. BROWN (**4**) came to the same conclusion in regard to a form of this species in which the antheridium did not fuse with the trichogyne. This conclusion was confirmed by the behavior of the chromosomes in the ascus. In *Lachnea* it would seem to be quite evident that there is no fusion of nuclei in the ascogonium, but there are appearances connected with division which may be readily mistaken for fusions. During prophase, when the nuclei are of course large, the massing of the chromosomes into a nucleolus-like group gives an appearance much like a fusion nucleus, while the reorganization of fusing nuclei in contact simulates fusing nuclei rather closely. Similar appearances have been seen by the writer (BROWN **4**) in *Pyronema*. In view of these facts and the increasing amount of negative evidence, it would

seem necessary to study the structure and behavior of the nuclei in the ascogonium quite closely before deciding that there is a fusion of nuclei in the ascogonium of any of the Pezizineae, and it is worthy of note that divisions have not been described in any of those mentioned above in which such a fusion is said to occur. This is particularly true of such an aberrant case as the occurrence of a second fusion following the sexual one in the life history of the same plant.

ALTERNATION OF GENERATIONS

When HOFMEISTER used the term alternation of generations, he of course did not know of the alternation of the haploid and diploid number of chromosomes, but meant the alternation of two kinds of plants, one of which bore sexual and the other asexual reproductive bodies. Since the significance of nuclear phenomena has come to be better understood, many writers have been inclined to use the term alternation of generations as synonymous with the alternation of the haploid and diploid number of chromosomes, but the question may be asked as to whether the two things always necessarily coincide. If we take the cases of *Alchemilla* (MURBECK **30**), which has an embryo sac with the diploid number of chromosomes, and *Nephrodium* (YAMANOUCHI **40**), which produces sporophytes with the haploid number, there is of course no alternation of the haploid and diploid number of chromosomes, but from the standpoint of phylogeny there is an alternation of two kinds of plants. In *Coleochaete*, where the zygospore divides to form a number of cells which produce zoospores, the cells formed from the zygospore may be regarded as an intercalated asexual phase, but reduction takes place at the first division of the zygospore (ALLEN **1**). Here there would seem to be, as FARMER has suggested, a sporophyte which normally has the same number of chromosomes as the gametophyte. In the red alga *Griffithsia bornetiana*, LEWIS (**25**) thinks that the sexual plants and the mass of carpospores constitute an antithetic alternation of generations, while the sexual and tetrasporic plants represent the alternation of an homologous phase. According to this interpretation, the diploid number of chromosomes would extend through two distinct phases.

It seems probable that the ascogonium in some of the ancestors of *Lachnea scutellata* was fertilized, and that this ended the gametophytic phase and initiated the sporophytic, which ended in the production of spores. According to the interpretation usually applied to the delayed nuclear fusion in the rusts, the above interpretation would hold even if nuclear fusion was delayed, as CLAUSSEN (**8**) claims to be the case in *Pyronema confluens*, until the formation of the ascus.

From a phylogenetic standpoint, it would seem reasonable, therefore, in the case of *Lachnea scutellata* to regard the stages from the spore to the ascogonium as gametophytic, and those from the formation of the ascogenous hyphae to the production of spores as sporophytic. The diploid number of chromosomes exists, however, only in primary nucleus of the ascus. Even if we should adopt DANGEARD'S (**10**) interpretation, and regard the ascus as an oogonium, the third division in the ascus, which shows the haploid number of chromosomes, would still appear to belong to the sporophyte. It would seem advisable, therefore, in the case of *Lachnea scutellata*, as in those previously mentioned, to distinguish between the alternation of generations and the alternation of the haploid and diploid number of chromosomes. The gametophyte is usually regarded as beginning with the spore mother cell, but if the ideas brought forward here are correct, this can hardly be the case in *Coleochaete* or *Lachnea scutellata*, and it would seem better to think of it as beginning with the spore.

Summary

The mature ascocarp of *Lachnea* is disk-shaped. The hymenium forms the upper surface, while the rim and lower surface are covered by a thick-walled cortical layer. The center is composed of rather loosely interlacing hyphae.

The ascogonium is the penultimate cell of a row of about nine.

The ascogonium is early surrounded by vegetative hyphae, the outer of which form the first part of the cortex, while those around the ascogonium remain active and give rise on one side to more of the cortex and on the other to hyphae which will produce paraphyses. When a part of the cortex is once formed, the develop-

ment of the hyphae composing that part ceases. The cells between the cortex and hymenium, however, remain active and add to the cortex and to the hyphae which produce paraphyses.

The ascogenous hyphae are large and branch profusely. At the ends of these are formed typical hooks, consisting of binucleate penultimate and uninucleate ultimate and antepenultimate cells. The two nuclei of a penultimate cell may fuse to form the nucleus of an ascus, or they may divide and give rise to the four nuclei of another hook. The uninucleate ultimate cell usually grows down and fuses with the antepenultimate cell, after which the two nuclei may give rise to the nuclei of another hook, or they may fuse to form an ascus.

When the hymenium is first formed, it is covered by the younger setae of the cortex, but as its diameter is increased and its level raised by the multiplication of the number of asci and paraphyses, it comes to be exposed.

No fusion of nuclei was observed in either the ascogonium or ascogenous hyphae, except where two nuclei fuse to form the primary nucleus of an ascus.

The nuclei of the ascogonium and ascogenous hyphae appear to be entirely similar except for size, and the same number of chromosomes, five, persists throughout their divisions. When the chromosomes are first formed, they are frequently grouped in a mass resembling a second nucleolus. The chromosomes become connected with a centrosome which was not apparent during the resting stage. This centrosome divides, and the two daughter centrosomes come to be situated at the poles of the spindle. At metaphase the five chromosomes divide, and at anaphase five pass to each pole. The daughter nuclei are usually organized at some distance from each other, but sometimes they are so close together that they resemble fusing nuclei.

The first division in the ascus is heterotypic. Synizesis is produced by the contraction of a single spireme. After synizesis the spireme splits longitudinally. The two halves come together again, after which the spireme contracts considerably and segments into five elongated chromosomes. A centrosome makes its appearance on the nuclear membrane and becomes connected with the chromo-

somes by linin fibers in the nucleus. The centrosome divides and the daughter centrosomes come to be situated at the poles of the spindle. The chromosomes divide transversely. As they approach the poles they appear to split longitudinally. The second and third divisions in the ascus are similar to those in the ascogonium.

The spore wall does not appear to be formed by the fusion of astral rays.

The writer wishes to express his thanks to Professor D. S. JOHNSON for helpful suggestions and criticisms, to Professor C. B. DAVENPORT, Director of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, for courtesies shown him during his stay at Cold Spring Harbor, to Mr. L. W. SHARP for help in collecting material, and to Dr. F. H. BLODGETT for assistance in the preparation of the photographs.

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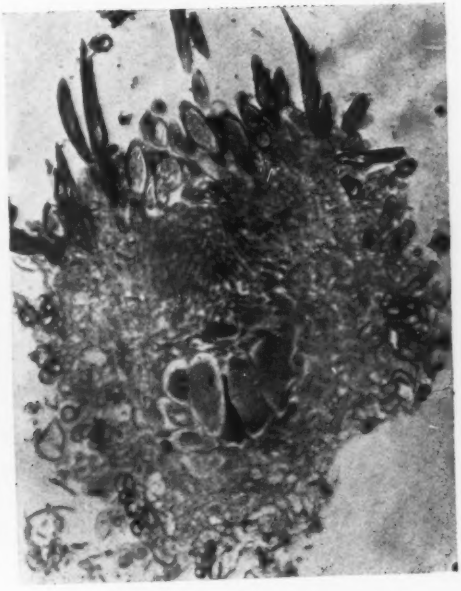

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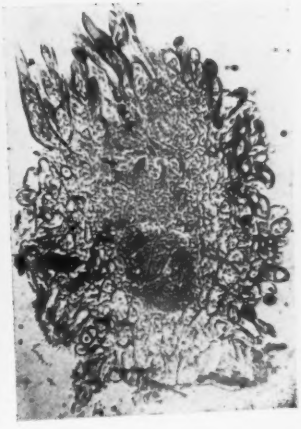

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EXPLANATION OF PLATE IX

FIG. 1.—Vertical section of mature ascocarp.

FIG. 2.—Vertical section of young ascocarp, showing young archicarp surrounded by comparatively few vegetative hyphae.

FIG. 3.—Vertical section of older ascocarp, showing ascogonium giving off ascogenous hyphae.

FIG. 4.—Vertical section of ascocarp, showing early stage in formation of hymenium.

PHYSIOLOGICAL BEHAVIOR OF ENZYMES AND CARBOHYDRATE TRANSFORMATIONS IN AFTER-RIPENING OF THE POTATO TUBER

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 148

CHARLES O. APPLEMAN

Introduction

An active growing period, followed by a period of rest, is a very general phenomenon among plants. Thus most seeds, tubers, and bulbs are structures whose growth processes have been arrested. Germination is simply a continuation of growth after the awakening from the rest period. The buds of the potato tuber, for example, will not grow, under the most favorable conditions, for several weeks after maturity; but after the awakening from this dormant condition they will grow under much less favorable conditions in a cold cellar.

Certain changes occur during the apparent dormancy, which are antecedent to the release of the growth processes, and these changes are known as "after-ripening." In many seeds the rest period is due to coat characters, which exclude or limit the supply of water or oxygen. After-ripening in such cases are processes which render the coats permeable to these substances. Often the processes of after-ripening are metabolic in character; this is especially true of tubers.

Certain external agencies artificially applied have been found to accelerate the processes of after-ripening, and thereby greatly shorten the natural rest period. MÜLLER-THURGAU (1) has shown that exposure to 0° C. for one month has this effect upon the resting potato tuber. Changes are thus brought about which break the rest period and allow growth to proceed several weeks earlier than under ordinary circumstances. He also found a great reduction of respiration, accompanied by an accumulation of sugars during exposure at low temperature.

The following work is a further study of the metabolic changes

occurring in the potato tuber as after-ripening proceeds during storage at 0° C. It is intended to throw some light upon the nature of the limiting factor or factors of growth during the rest period of this particular organ. Thus far a quantitative study has been made of digestive and respiratory enzyme changes and the carbohydrate food transformations.

Material

The material used for this investigation was the red land potatoes grown in Texas and procured only a few days after being harvested. This variety has a very short rest period. Two crops a year are grown in this climate, and samples from both crops were used in this work. The tubers were wrapped with paraffin paper and one-half stored at 0° C. and the remainder stored in a dark basement room at 20–25° C.

Methods

GLUCOSE, SUCROSE, AND STARCH.—The methods employed for the determinations of glucose, sucrose, and starch were virtually those of the association of official agricultural chemists (**7**). The glucose was determined according to the method of MUNSON and WALKER.

DIASTASE.—A modification of the starch iodine method (**8, 9**) was used in making the diastase determinations. One cc. of a 1 per cent soluble starch solution was placed in each of 10 test tubes surrounded with ice. Ascending amounts of the potato extract, prepared by grinding with quartz sand and filtering, were added to the tubes, beginning with 1 cc. and increasing the amount 0.1 cc. for each succeeding tube. The tubes were then incubated at 40° C. for 48 hours, placed again in ice, filled nearly full with water, and 3 drops of iodine solution added to each tube. The first tube in the descending series which showed a blue or violet color was considered the index for comparative diastatic activity. The method is impractical with larger amounts of extract on account of dark oxidation products and the precipitate which falls on addition of the iodine. If small amounts of both starch solution and extract are used, and the incubation continued for

48 hours, satisfactory duplicates may be obtained, so the method was considered sufficiently reliable for comparative purposes. A few drops of toluol were added to each tube during incubation, to insure against activity of bacteria.

CATALASE.—A detailed description of the method for the catalase determinations will be found in a recent paper by the author published in this journal (4). In all cases the water bath temperature was 25° C. during the experiment.

PEROXIDASE.—In order to compare the rate of peroxidase activity in the material under investigation, various methods were tried and variously modified. The methods differed mainly in the preparation and treatment of the extract, for in all cases guaiaconic acid was used as the oxidizable substance (10, 11). A definite quantity of extract was allowed to act upon a definite quantity of guaiaconic acid in the presence of hydrogen peroxide. The time required for the oxidation of the guaiaconic acid to reach a depth of blue equal to that of a standard tube, containing a solution of indigo carmine, was considered the index of the peroxidase activity. The standard tube was placed against a white background and screens arranged to eliminate shadows and unequal lighting. If the test tube is held against the standard tube, and the eye fixed upon the line separating the tubes, and the time noted when the color is the same on both sides of the line or when the line seems to disappear, quite accurate readings may be obtained with a little practice. The error of reading is greatly reduced if the test solution is of such dilution or the standard tube of such depth of blue that the time of reaction is not less than ten seconds nor greater than one minute. If the solution of indigo carmine is made up with pure distilled water, the fading of color at the end of several weeks is so slight that it falls well within the experimental error involved in comparing the shades of blue.

The present methods for peroxidase determinations are unsatisfactory, but under careful manipulation the above method will give results of value for determining comparative activity of the guaiaconic acid oxidizing peroxidase in potato tubers.

The method described by GRÜSS (2) for obtaining a peroxidase solution from the potato tuber was first tried. According to this

method, morphologically similar parts of the tuber were sliced directly into absolute alcohol and heated to 70° C. for 10 minutes in order to destroy the oxidases. The slices were allowed to remain in alcohol 24 hours. The alcohol was changed three times. They were then dried between filter paper, covered with ether for a few minutes, replaced between filter paper, quickly dried in a vacuum desiccator, and thoroughly pulverized in a mortar. One gram of this powder was ground one minute with quartz sand and 25 cc. water and filtered. For the tests 5 cc. of the filtrate were used and 0.5 cc. of guaiaconic acid solution and 0.1 cc. of one-half per cent hydrogen peroxide. The guaiaconic acid solution was prepared by dissolving 0.5 gram of guaiaconic acid in 50 cc. alcohol.

Three sources of error were soon discovered in this method of extract preparation, which render it unreliable for comparative purposes. Filtering, which is necessary in order to obtain a sufficiently clear solution for colorimetric work, removes a large percentage of the peroxidase. This is probably due to inclusion of the peroxidase in the clot of coagulable proteins, and not to an insoluble form of the enzyme. Filtering has no effect on the peroxidase activity of fresh unheated extract.

TABLE I

EFFECT OF FILTERING ON PEROXIDASE ACTIVITY OF HEATED EXTRACT

HEATED TO 70° C. for 10 MIN.	SECONDS REQUIRED FOR REACTION TO REACH STANDARD TUBE		
	Unfiltered	Filtered through cotton	Filtered through paper
Sample 1	..	28	56
Sample 2	..	12	25
Sample 3	15	..	45
Sample 4	15	..	35

Another source of error probably arises also from the presence of coagulable proteins. The peroxidase leaches out of the coagulum and thereby renders the peroxidase activity of the solution very unstable, as shown in table II. HASSELBRING and ALSBERG (5) found a similar condition in studies upon oxidases, and first concluded that it must be due to coagulable proteins.

It is not due to activation of zymogen, as the phenomenon does not occur in the fresh unheated extract method described later.

TABLE II

SHOWS INCREASE IN PEROXIDASE ACTIVITY OF SOLUTION ON STANDING

	SECONDS REQUIRED FOR REACTION TO REACH STANDARD TUBE		
		After 2 hours	After 24 hours
Slices of potato dehydrated with alcohol and ether; heated to 70° C. for 10 min.	51	34	30

A third source of error, which would have to be taken into account, is the degree and time of drying. If the slices are dried in a desiccator for several hours, the peroxidase activity is greatly impaired. After a few days the peroxidase is practically destroyed in the powder produced by grinding the dried slices (table III). GORTNER (**6**) has recently described a tyrosinase, which loses its vitality on drying.

TABLE III

SHOWS LOSS OF PEROXIDASE IN POTATO WITH DRYING

Potato tuber	Time required for reaction to reach blue of standard tube
Slices dried in desiccator 30 min.	24 seconds
Slices dried in desiccator 22 hrs.	120 seconds
Powdered slices standing 4 days exposed to laboratory air	10 minutes

The above facts alone are sufficient to render the method described by GRÜSS of little value for determining peroxidase activity in conditions approaching those of the living tuber. By grinding the potato tuber with $CaCO_3$, thus neutralizing the acids, the peroxidase activity was found to be quite stable for some time in the resulting extract (table IV).

Based upon this fact the following procedure was employed for the final comparative determinations of the peroxidase in the potato tubers under investigation. The tubers were grated with frequent dipping of the surface in $CaCO_3$. The pulp was then

ground in a mortar with quartz sand for two minutes, and the extract pressed through cotton and cheesecloth; 1 cc. of the extract was at once added to 300 cc. of water. This dilution gave a solution sufficiently clear for the test and a speed of reaction which reached the standard color in less than a minute. It was unnecessary to destroy the oxidase by heating. In this dilute solution the time required for the oxidase to produce a visible blue was longer than that required for the peroxidase to produce the blue of the standard color.

TABLE IV

EFFECT ON PEROXIDASE ACTIVITY OF EXTRACT WHEN THE POTATO TUBER IS GRATED WITH $CaCO_3$

POTATO TUBER	SECONDS REQUIRED FOR REACTION TO REACH BLUE OF STANDARD TUBE		
		After 6 hours	After 24 hours
Ground with $CaCO_3$	21	21	30
Ground without $CaCO_3$.....	45	..	90

OXIDASE.—Colorimetric methods, as well as the direct measurement of the oxygen consumed by the oxidation of hydrochinon in the manner recommended by GRÜSS (**2**), were used in an effort to ascertain the comparative rate of oxidase activity. So many sources of error were discovered in applying these methods to the material under investigation, that the results were considered too unreliable for publication. Better methods than those in present use are much needed.

Experiments

In comparing results obtained by the two methods for peroxidase determinations previously described, it was found that the alcohol and ether method always gave a much greater peroxidase activity in the cold storage potatoes than in those stored at room temperature, while the fresh extract method gave practically the same in both cases during the same period of storage. According to the following table this would seem to be due to an alteration at low temperature of coagulate protein, which modifies the

amount of peroxidase occluded by clot, for after 24 hours of leaching the activity is just as great in the room-stored potatoes.

TABLE V

SHOWS INCREASE IN PEROXIDASE ACTIVITY IN COLD STORAGE POTATOES BY THE ALCOHOL AND ETHER METHOD, BUT NO INCREASE WHEN THE TESTS ARE MADE WITH FRESH UNHEATED EXTRACT

POTATO TUBER	SAMPLE	SECONDS REQUIRED FOR REACTION TO REACH STANDARD COLOR			
		Storage at 20°–25° C.		Storage at 0° C.	
			After 24 hours		After 24 hours
Slices treated with alcohol and ether; heated to 70° C. in alcohol for 10 minutes	1	60	20	25	20
	2	56		21	
	3	51		32	
Ground with $CaCO_3$ and determinations made with fresh unheated extract	1	35	42	35	40
	2	31		30	
	3	32		25	

The following table is a summary of the metabolic changes thus far studied occurring in a typical lot of young potatoes stored at 0° C. and 20–25° C. for a period of 6 weeks, tests being made every 2 weeks. Several lots were run, but as they all showed practically the same changes, only a typical table is given.

TABLE VI

SHOWS METABOLIC CHANGES OCCURRING IN POTATO TUBERS DURING AFTER-RIPENING AT LOW TEMPERATURE

EXPOSURE	TEMPERATURE	GLUCOSE	SUCROSE	STARCH	DIASTASE	CATALASE	PEROXIDASE
Days	° C.	Per cent	Per cent	Per cent	cc. potato extract to digest 100 cc. starch sol. in 24 hrs. at 48° C.	cc. of O_2 evolved in 3 min.	Seconds required to reach standard color
14	20–25	0.37	0.55	14.4	30	40.6	35
	0–+1	0.52	1.3	13.2	25	37.6	35
28	20–25	0.32	0.54	14.	30	41.2	33
	0–+1	1.8	1.65	11.	20	28.6	32
42	20–25	0.3	0.84	13.6	25	44.	32
	0–+1	3.5	1.8	9.6	20	26.4	25

Potatoes stored at 0° C. or below exude an acid fluid. This fact suggested the possibility that the increased diastatic activity after cold storage may be due to free acids. The decreased catalase activity might also be thus accounted for. The following single experiment is evidence in favor of this view.

Two potatoes of nearly equal weight were grated and thoroughly ground, one with $CaCO_3$, and the other without. Both were stored at 0° C. for 34 days, and analysis made according to table VII.

TABLE VII

EFFECT OF STORAGE AT 0° C. FOR 34 DAYS WHEN POTATO IS PREVIOUSLY GROUND WITH AND WITHOUT $CaCO_3$

POTATO GROUND	GLUCOSE	DIASTASE	PEROXIDASE	CATALASE
	Per cent	Units of extract to digest a unit of starch	Seconds required to reach standard color	cc. of O_2 evolved in 3 min.
Without $CaCO_3$	0.18	100	30	0.1
With $CaCO_3$	trace	160	40	6.7

The expressed potato sap is strongly acid. After repeated titrations, I found that the sap from cold storage potatoes and that from room-stored ones contained practically the same amount of acid. Low temperature, therefore, does not change the total acidity, but probably affects the permeability of protoplasmic membranes, and thereby allows the acids to reach zymogens more rapidly than under normal conditions.

Conclusion and summary

The method recommended by GRÜSS for determining the rate of peroxidase activity in the potato tuber gives no indication of the rate of activity in conditions approaching those of the living tuber. This is due to errors introduced by inclusion of the peroxidase in the clot of coagulable proteins, and to the loss of peroxidase during the process of drying the slices. After a few days the peroxidase is practically destroyed in the dry powdered potato. This method always showed an apparent increase in peroxidase activity in cold storage potatoes. The evidence at hand seems to indicate that this is due to an alteration of coagulable proteins

by low temperature, thus modifying the amount of peroxidase occluded by the clot.

Certain internal changes are accelerated by 0° C., which shorten the rest period of potato tubers.

Both glucose and sucrose accumulate. The increase in sucrose is more rapid at first than glucose, but by the end of 6 weeks of storage at low temperature the percentage of glucose is about twice that of sucrose.

Diastase activity was greater in the cold storage tubers than in those stored at room temperature at the end of 2 and 4 weeks; but at the end of 6 weeks there was no appreciable difference, as the variety used for this work was near the end of the rest period. A few had already germinated. The increased diastase activity is probably due to greater activation of zymogen by free acids, which are liberated by the greater permeability of protoplasmic membranes at low temperatures.

Catalase is very abundant in potato tubers stored either at 0° C. or at room temperature, but suffers a gradual reduction as storage at 0° C. continues. The presence of free acids would cause this reduction, as catalase is rapidly destroyed by the free acids in ground potato pulp. This behavior of catalase corresponds with that of respiration under similar conditions, a significant fact in the light of a recent claim (3) that catalase is the primary factor in alcoholic fermentation, and therefore probably in respiration.

A guaiaconic acid peroxidase is very active in potato tubers at the beginning of the rest period and increases slowly as the end of the rest period approaches. Low temperature had no appreciable effect in hastening this increase in the material used for this work, according to the method employed for its determination.

The changes peculiar to after-ripening may be in the buds, and the metabolism of the tuber as a whole may bear little or no causal relation to these processes.

The writer wishes to acknowledge his indebtedness to Dr. WILLIAM CROCKER for suggesting the problem and for his untiring interest and assistance during the progress of the work.

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CURRENT LITERATURE

NOTES FOR STUDENTS

Morphology of Nidularia.—In two papers FRIES has given a clear account of the morphology of the fruit-body and spore development of *Nidularia pisiformis* Tul. The first paper deals with the development of the fruit-body.[1] The youngest stages observed are nodules about 0.4 mm. in diameter. In the earliest stages these are differentiated into a uniform medulla and a cortex which become more pronounced later. All the cells are binucleate. The medulla soon becomes differentiated into a lower sterile portion and an upper denser portion in which the peridiola arise. The beginning of the peridiola is indicated by the appearance of islets of hyphae, rich in protoplasm, growing toward common centers. These hyphae represent the young hymenium. Later a cavity is formed by the expansion of these hyphae and those of the subhymenial layer. The peridiola, spherical at first, assume an oval form. A wall is formed around them, but this at first remains open at the poles. Through the openings the peridiola remain in connection with the surrounding medulla during their growth; the wall finally incloses the whole peridiolum. The development agrees in the main with the development of the fruit-bodies of other members of this peculiar group of Gasteromycetes, except that the peridiola are not connected to the wall of the fruit-body by strands of hyphae as in *Crucibulum* and *Cyathus*.

In the second paper[2] an account of spore development of the same plant is given. The young basidia are binucleate, agreeing in this respect with other Basidiomycetes, as well as with the ascus of Ascomycetes. The two nuclei grow to about twice the size of the vegetative nuclei, after which fusion takes place. This is followed by the usual rapid growth of the fusion nucleus just previous to the divisions leading to spore formation. The chromatin, which is in the so-called synapsis stage, later spreads out through the nuclear cavity in the form of an irregular band, which is single at first, but later appears to split lengthwise into two parallel threads. The chromatin thread shortens and thickens and breaks up into a number of double chromosomes. This process was not easily made out, but the author is inclined to believe that two such double chromosomes are formed, although some earlier stages seemed

[1] FRIES, ROB. E., Om Utvecklingen af Fruktkroppen och Peridiolerna hos *Nidularia* (with German résumé). Svensk. Bot. Tidsk. **4**:126–138. *pl. 1. fig. 1.* 1910.

[2] ———, Ueber die cytologischen Verhältnisse bei der Sporenbildung von *Nidularia*. Zeitschr. Bot. **3**:145–165. *pls. 2.* 1911.

to show three to five segments. The spindle of the first division is transverse to the long axis of the basidium, as in the whole series of Basidiomycetes, beginning with the Tremellales. The processes of division are very obscure, but there appeared to be three or four chromosomes at each pole in the anaphase. The author interprets this as a heterotypic division, but believes that during the division the components of the double chromosomes become separated, thus accounting for the presence of four instead of two at each pole. The second division proceeds without reorganization of the daughter nuclei. It results in the distribution of the components of the double chromosomes to the new nuclei. Two chromosomes appear at each pole of the spindles. The whole interpretation hinges on the correctness of the author's assumption that only two segments are formed from the double chromatic band after synapsis.

After the reorganization following the second division of the nuclei, the sterigmata bud out from the basidia and swell out into spore bodies. Then the peculiar process of migration of the nuclei into the spore bodies takes place. The nuclei move to the upper part of the basidium and lose their membranes, leaving only the nucleolus and chromatin. The chromatin thread, with the nucleolus at its apex, then migrates through the narrow sterigmata into the spore cavity. This peculiar migration is explained by the fact that during the process the nuclei are in the prophase of a division which is completed as soon as the chromatin has entered the spore cavity. The mature spore is binucleate, corresponding in this respect with other Gasteromycetes that have been investigated.—H. HASSELBRING.

Hereditary factors in Primula.—The existence of numerous varieties of the Chinese primrose (*Primula sinensis*) makes this species an enticing one for the study of unit characters in inheritance, but the number of different factors is so great as to make complete analysis practically impossible. Factors for form of foliage, heterostylism, singleness of the flower, color of stems, color of flowers, palliators, inhibitors, pattern factors, coupling, and repulsion, are all needed in the description of the results. During the past eight years BATESON and GREGORY have been analyzing the characters which distinguish the different varieties, and they have jointly and severally reported on various phases of their results from time to time since 1903. GREGORY[3] has just presented a comprehensive memoir on these experiments, illustrated with three excellent double plates, two colored and one photographic. Some of the more interesting results may be mentioned. Long style is epistatic to short style; palmate type of leaf to the pinnate or "fern" type; crenate margins to entire margins; single flowers to double; the flower colors may be arranged in a series in such manner that each is epistatic to all that follow, as follows: dominant white, magenta, red, blue, recessive white; some pale

[3] GREGORY, R. P., Experiments with *Primula sinensis*. Jour. Genetics 1:73–132. *pls.* 3. 1911.

colors are recessive to the full colors, but more commonly the lighter shades are epistatic to the intense ones and are interpreted as the result of a partial inhibitor or "palliator"; there is similar epistasis of the lighter stem colors to the darker; two inhibiting factors produce definitely localized effects in the flower, one affecting the central region of the flower, the other the periphery. In all of these unit characters the expected Mendelian ratios were obviously present except in several instances of "repulsion" and of partial coupling. Thus magenta was never found associated with the short style, and a partial coupling between magenta flower color and green stigma seems to indicate that there is a segregation on the plan 7:1:1:7 in one of the sexes, while in the other sex the segregation follows the usual plan 1:1:1:1.

The occurrence of dominant and recessive white in the flower color of the different varieties presents an interesting situation. In the varieties first investigated, the dominant white was always associated with red stems and the recessive white with green stems. An exception to this rule exists in the case of the variety "Pearl," in which dominant white and green stems are combined. KEEBLE and PELLEW[4] now report an exception in the opposite direction in "Snow King," a red-stemmed variety with either dominant or recessive white flowers. Crosses between this variety and various colored varieties gave different results according as the particular individual of "Snow King" used in the cross chanced to be dominant, heterozygous, or recessive in regard to a dominant white factor *W*. The heterozygous whites when crossed with colored varieties gave white and colored, 1:1 in the F_1, and these F_1 whites when self-fertilized produced an F_2 which in each case closely approximated the expected ratio, 13 white: 3 colored.—GEORGE H. SHULL.

An inhibiting factor in oats.—NILSSON-EHLE[5] describes a number of instances in which mutants resembling the wild oats (*Avena fatua*) have appeared in his cultures of numerous cultivated varieties of *Avena sativa*, the coefficient of mutation being about 1 in 10,000. These atavists had approximately the same congeries of characteristics regardless of the characteristics of the varieties in which they were discovered. Most frequently they were found in heterozygous combination with the cultivated varieties, but sometimes also in the pure extracted forms. That these could not have been the results of crosses with the wild oats is proved by the fact that when they appeared in a variety having white or yellow glumes, the atavist retained this recessive character. The heterozygotes proved to be in all cases intermediate between the atavists and the particular varieties in which they appeared. The fact that the atavistic type differs in each case by a single unit character, so that the whole group of wild characters appears in their

[4] KEEBLE, F., and PELLEW, MISS C., White-flowered varieties of *Primula sinensis*. Jour. Genetics **1**:1–5. 1910.

[5] NILSSON-EHLE, H., Ueber Fälle spontanen Wegfallens eines Hemmungsfaktors beim Hafer. Zeit. Ind. Abstam. Vererb. **5**:1–37. *pl. 1*. 1911.

usual combination in one-fourth of the F_2 offspring, leads the author to the conclusion that the difference between the wild oats and these various cultivated varieties is due to the presence in the latter of an inhibiting factor which prevents the development of the wild characters. As he has never found among the numerous crosses he has made between different cultivated varieties any instance in which the atavists made up one-sixteenth of the F_2, as they should do if different varieties possessed different inhibiting factors, he concludes that the same inhibiting factor is present in all the cultivated varieties, and that the different degrees of development of the awns and hairiness of the glumes which have been found to be dependent upon independent genes, must remain latent in the wild oats until the origin of an inhibiting factor brings them to light. On this ground he argues that the degree of discontinuity which results from any mutation depends upon the number of latent genes which are brought into manifestation by it, and also that various apparent correlations may result from the disappearance of a factor which had simultaneously inhibited both of the characters which appear to be correlated. The author does not take into account the hypothesis of "variable potency," which could also be made to explain how the same inhibiting factor in the various cultivated varieties could produce such various degrees of development of awns, hairiness of the glumes, etc., as are displayed by them.—GEORGE H. SHULL.

Mitosis in Spinacia.—This extensive investigation by STOMPS,[6] written in Dutch, but with an eleven page résumé in German, deals with mitosis in both vegetative cells and in the microspore and megaspore mother cells.

The *2x* generation shows 12 chromosomes arranged in pairs, which can be distinguished not only in the nuclear plate but also in the prophase, and pairs probably persist in the resting nucleus. No continuous spirem is formed, the two components of each pair, as soon as they can be distinguished, having two free ends. A longitudinal splitting of the chromosome occurs in early prophase, a longitudinal row of vacuoles appearing, and these, by increasing in size, split the chromosome. This mode of splitting results in threads with alternating thickened and slender portions, but STOMPS does not regard the thickened portions as chromomeres or ids, nor does he regard the slender portions as linin, but both are the same in substance.

In the prophase of the reduction division, before synapsis, the 12 chromosomes fuse in pairs, forming 6, each with two free ends. There is not only a pairing, but also a genuine fusion of the two chromosomes of each pair. No continuous single or double thread is formed. As the nucleus comes out of synapsis, one sees 6 chromosomes, each evidently double, and the two mem-

[6] STOMPS, THEO. J., Kerndeeling en Synapsis bij *Spinacia oleracea*. 8vo. pp. 162. *pls. 2*. 1910. A briefer account in German, which is partly a summary and partly a translation of the original, is published in Biol. Centralbl. **31**: 257–320. *pls. 1–3*. 1911.

bers of a pair may separate at this stage. Tetrads sometimes occur at this time. The mantle fibers (*Zugfasern*) are believed to persist from one cell generation to another. The nuclear membrane is a tonoplast, and the nuclear cavity a complex of vacuoles.

Many of the figures look rather diagrammatic, but they are carefully drawn, and the summary indicates that the author, at least, feels certain of his principal conclusions. The work is so extensive and so well presented that it cannot be laid aside; cytologists should either confirm the conclusions or correct them.—CHARLES J. CHAMBERLAIN.

Fungi in rhizoids of liverworts.—Investigation of about thirty species of liverworts by GARJEANE[7] shows that there is no uniformity in the occurrence of fungi in the rhizoids. In some forms the presence of fungi seems to be the rule; in others, especially the bark-inhabiting forms, their presence seems to be the exception. In the same colony individuals with infected rhizoids often occur together with others not infected. The details of the mode of growth of the hyphae are described for *Lophozia inflata* and species of *Cephalozia* and *Cephaloziella*. From the details it appears that the plants in no way profit as a result of the presence of fungi in their rhizoids. On the contrary, the protoplasm in the young rhizoids, and also in the neighboring cells when these are infected, is killed by the fungi. Extended infection of rhizoids is accompanied by sickening of the plants. An interesting reaction of the rhizoids to the attack of the fungus is described in *Lophozia*. When the hypha comes into contact with a rhizoid, a thickening appears on the inside of the rhizoid wall opposite the point of contact. As the hypha grows into the cell, cellulose is continually deposited ahead of the growing point, so that the hypha is surrounded by a sheath of cellulose. Often hyphae pass straight through rhizoids in this way, and become incased in a tube of cellulose. The author was successful in isolating the same species of fungus, described as *Mucor rhizophilus*, from nine species of liverworts. A large number of successful infections was made with this fungus in sterile cultures of *Lophozia inflata*, *Cephalozia bicuspidata*, *Cephaloziella* sp., and *Jungermannia ventricosa*. The author believes that the association of fungus and rhizoid is not of the nature of a mycorhiza; neither does the fungus cause considerable damage to the plant, although strongly infected plants show the unfavorable influence of the fungus.—H. HASSELBRING.

Fall of petals.—FITTING[8] finds that a number of stimuli will cause the premature falling of the corollas of various sympetalous and polypetalous flowers. He worked in the main, however, with *Geranium pyrenaicum*. Among chemi-

[7] GARJEANE, A. J. M., Die Verpilzung der Lebermoosrhizoiden. Flora **102**: 148–185. *pls. 11, 12. figs. 9.* 1911.

[8] FITTING, HANS, Untersuchungen über die vorzeitige Entblätterung von Blüten. Jahrb. Wiss. Bot. **49**: 187–263. 1911.

cals that are effective are traces of illuminating gas and tobacco smoke; considerable concentrations of CO_2 (4–50 per cent); high partial pressures of ether and chloroform vapors; and HCl gas. Other effective stimuli are high temperatures, shaking, sprinkling with dust, and wounding the style. FITTING concludes that the process is a vital one, for it does not occur when the plant is in heat rigor or in rigor from lack of oxygen. He also concludes that it is a true stimulus process, showing well-marked presentation and reaction times, as well as typical summation and relaxation. The reaction cannot be attributed to general inhibitory and acceleration effects upon the flowering process, but is a direct stimulatory effect upon the petals. The reaction time varies greatly with the stimulus, age of flower, and species of flower. Traces of illuminating gas give a reaction only after 2–6 hours, while CO_2 in optimum concentration gave a reaction after 30 seconds in *Verbascum thapsiforme*, and after only a slightly longer period in a number of other forms. Reactions to shaking and high temperatures were also rapid. Old flowers were always more sensitive than young ones.

FITTING proposes to call these responses *chorisms*, using the prefixes chemo-, thermo-, seismo-, etc. The paper should prove of considerable economic interest.—WILLIAM CROCKER.

Fundamental units of vegetation.—Ecology as a definite branch of the science of botany, while still in its infancy, has reached a stage in its development at which it is instructive to take an occasional retrospective glance in order to inquire what were the beginnings from which the branch has developed and whether there are tendencies which require pruning or molding. MOSS[9] has taken such a backward look over the course of the development of the concepts and the nomenclature of the units of vegetation most used in the study of plant communities. The look has been a careful one, and has traced "plant associations" from its first use in a floristic sense by HUMBOLDT, in 1806, and with its truer ecological meaning by SCHOUW, in 1822, to the present day. To MOSS the concept seems to be best defined as "a community of definite floristic composition within a formation."

He finds "plant formation" a term and concept of slightly more recent origin, dating to its employment by GRISEBACH in 1838. The different meanings this term has had for various workers are discussed in such a manner as seems likely to lead to some agreement as to its proper content. The desirability of some general agreement as to methods of denoting associations and formations is discussed in a most reasonable manner, and several good suggestions made. The writer is to be commended for correctness of perspective and breadth of view throughout what is doubtless the best historical review of this phase of botany which has yet appeared.—GEO. D. FULLER.

[9] MOSS, C. E., The fundamental units of vegetation. New Phytol. **9**:18–53. 1910.

Tropic responses.—In working out the phototropic responses of *Avena sativa*, ARISZ[10] believes he has shown that the terms reaction time, presentation time, threshold of stimulation, etc., do not represent any well-determined end points in tropic responses. Quotations from his paper present his conclusions: "Each quantity of energy reacts on the plant and is expressed by a curvature of definite maximum strength." "If we once more trace how far the above investigations influence our conception of the process of stimulation, it is clear that the similarity to physico-chemical processes becomes more and more marked. The existence of a threshold of stimulation can no longer be maintained, for not only is each quantity of energy perceived, but it is clear now that a reaction will always take place. The time which intervenes between the application of the stimulus and the beginning of the curvature, the 'reaction time,' was found to be experimentally undeterminable. Thus the latter cannot serve as a measure of sensitivenesss."

We are urged, then, in this stronghold of stimulus physiology (tropisms), to abandon the stimulus conception for the physico-chemical. BLACKMAN had earlier urged such a shift of viewpoint in the study of metabolic processes of plants.—WILLIAM CROCKER.

The cytology of rice.—Since closely related species or even races of a given species may show differences in chromosome characters, several races of rice (*Oryza sativa*) were selected by KUWADA[11] for a cytological study. Just before synapsis in the pollen mother cell, a number of chromatin masses, about equal to the diploid number of chromosomes, are found scattered throughout the nuclear cavity. The masses, which are constantly paired, stretch out into double threads, which remain double during synapsis, but fuse after the synaptic stage is past. Soon after synapsis, the single thread arising from the fusion again becomes double and segments into 12 bivalent chromosomes, or gemini, and throughout the prophases the two parts of the bivalent chromosomes remain in parallel association, while they become shorter and thicker. Even in the homotypic division paired chromosomes, forming pseudogemini, occur. In the diploid generation the chromosomes are always paired and the number is 24. The development of the embryo sac presents nothing unusual. There are at first three antipodals, but, as in other Gramineae, the number becomes much larger at a later stage in the development.—CHARLES J. CHAMBERLAIN.

Physics of transpiration.—RENNER[12] has already shown that in still air evaporation from surfaces of like shape but different size varies more nearly

[10] ARISZ, W. H., On the connection between stimulus and effect in phototropic curvatures of seedlings of *Avena sativa*. Reprint from Proc. Konink. Akad. Wetensch. Amsterdam. March 25, 1911.

[11] KUWADA, YOSHINARI, A cytological study of *Oryza sativa* L. Bot. Mag. Tokyo 24:267–281. *pl. 8.* 1910.

[12] Rev. in BOT. GAZ. **51**:156. 1911.

in proportion to the like linear dimensions of the surfaces than in proportion to the surfaces. He has also shown that for equal surfaces isodiametric surfaces give least evaporation, and that the greater the deviation from the isodiametric the greater the evaporation. These facts are related to the water vapor cap over the evaporating surfaces, a thing to which RENNER gives great importance in the absence of air currents. He concludes that the deviation from the linear dimension law, under conditions cited in the first sentence, is in large part due to convection currents set up by the moist air over the evaporating surface being less dense than the surrounding dry air. In the present work,[13] by means of wet filters and water surfaces, RENNER studied in great detail the effect of shape, size, position, and proximity of evaporating surfaces in both still and moving air. Later he expects to carry these studies over to leaves, where the part played by internal regulation can also be determined.—WILLIAM CROCKER.

Theories of heredity.—In a discussion of two theories of heredity, that the nucleus is and that it is not the sole bearer of hereditary qualities, LUNDEGÅRD[14] devotes most of his space to a study of the literature, but also describes the various constituents of the cell in root tips of *Vicia Faba*. In the first part of the paper he comes to the conclusion that the nucleus cannot be the sole bearer of hereditary characters, but that extra-nuclear structures must be considered. To the reviewer, the arguments do not seem conclusive. The second part deals with the structures variously known as mitochondria, chondriomitria, chondriosomes, etc., and with plastids and other bodies and substances found in cells. He believes that the mitochondria do not come from the nucleus, and that they are not bearers of hereditary qualities. Here again the reviewer is not convinced and, in the present state of the subject, is inclined to think that at least some of the bodies known as mitochondria are of nuclear origin. Plastids also are considered, and the view of SCHIMPER and others, that the plastid is a permanent organ of the cell, is upheld.—CHARLES J. CHAMBERLAIN.

Heterochromosomes.—That there is a differentiation among chromosomes has been recognized for some time by zoologists, but it is only more recently that botanists have turned their attention to the subject. In the wild mulberry (*Morus indica*) TAHARA[15] finds, in early stages of prophase in sporophyte nuclei, paired chromatin masses which may be called pronuclei, and even at

[13] RENNER, O., Zur Physik der Transpiration. Ber. Deutsch. Bot. Gesells. **29**: 125–132. 1911.

[14] LUNDEGÅRD, HENRIK, Ein Beitrag zur Kritik zweier Vererbungshypothesen. Ueber Protoplasmastrukturen in den Wurzelmeristemzellen von *Vicia Faba*. Jahrb. Wiss. Bot. **48**: 285–378. *pls. 6–8*. 1910.

[15] TAHARA, MASATO, Ueber die Kernteilung bei *Morus*. Bot. Mag. Tokyo **24**: 281–289. *pl. 9*. 1910.

this early stage two pairs are noticeably larger than the rest, and the difference becomes more pronounced as the chromosomes become arranged in the equatorial plate. The usual number of chromosomes is 28, but it is often higher. In the mother cells there are constantly 14 bivalent chromosomes, or gemini, one pair constantly larger than the rest. While zoologists are assigning the large chromosome a particular function in the determination of sex, it is too early to make any statement for plants. At present what is needed is extensive investigation along the lines of the present paper.—CHARLES J. CHAMBERLAIN.

Crown gall and sarcoma.—In a recent review[16] of the bulletin on crown gall by SMITH, BROWN, and TOWNSEND, attention was called to the resemblance of the crown gall tumors to certain malignant animal tumors. SMITH has now issued a brief circular[17] to announce the discovery of further evidence of this resemblance. The bacterium causing the primary tumor occurs also in the secondary tumors, associated with the tumor cells, the conclusion being that this is not a disease which propagates itself independently of the inciting organism. Furthermore, "tumor strands" were observed connecting primary and secondary tumors, being deep-seated offshoots from the primary tumor which wedge their way through stems and leaves like foreign bodies and give rise to secondary tumors, which subsequently rupture through to the surface of the plant. The full details, with illustrations, are promised in another bulletin.—J. M. C.

Symposium on reproduction.[18]—At the meeting of the Botanical Society of America held at Boston, December 27–31, 1909, a symposium on the nuclear phenomena of sexual reproduction was one of the features. Dr. DAVIS discussed the nuclear phenomena of sexual reproduction in the algae, and Drs. HARPER, CHAMBERLAIN, and MOTTIER discussed the subject in the fungi, gymnosperms, and angiosperms respectively. No new investigations were presented, since the object was not to record the results of recent personal research, but rather to present the subject in such a way as to make it helpful to the botanical public, and to stimulate and facilitate research in the various phases of the problem. Naturally, the principal emphasis was laid on fertilization and reduction of chromosomes. No serious differences of opinion appeared, except in regard to alternation of generations.—CHARLES J. CHAMBERLAIN.

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[16] BOT. GAZ. **52**:75. 1911.

[17] SMITH, ERWIN F., Crown gall and sarcoma. U.S. Depart. Agric., Bur. Pl. Ind., Circular no. 85. pp. 4. June 20, 1911.

[18] DAVIS, B. M., HARPER, R. A., CHAMBERLAIN, CHARLES J., and MOTTIER, D. M., Nuclear phenomena of sexual reproduction in thallophytes and spermatophytes. Publication 45 of The Botanical Society of America. Reprinted from the American Naturalist of June, July, September, and October, 1910.

Germination of fern spores in darkness.—It has been almost the universal experience of those who have investigated the germination of fern spores that at usual room temperature and with so-called inorganic nutrition they will not germinate in complete absence of light. However, at high temperature, or in sugar or peptone solutions, germination in total darkness has been induced. FISCHER[19] has now found that the spores of one of the commonest and most widely distributed ferns, *Polypodium vulgare*, are able to germinate in darkness at 25° just as well as in light. This is probably the best case on record for germination in darkness, since prothallia were actually obtained, and not merely a bursting of the exospore, as LAAGE reported for *Osmunda regalis* and other ferns. The prothallia formed in darkness differ somewhat from those of the same age produced in light, being composed of more and longer cells. It is probable that some limiting factor prevents the germination of the spores of most ferns in darkness; and discovery of the proper conditions for germination may show that the spores of many species are capable of developing prothallia without light.—CHARLES A. SHULL.

Vegetation of Nockamixon Rocks and Navesink Highlands.—It is important to have on record the natural vegetation of areas that are becoming densely populated, since tracts that have escaped the modifying influence of the ax and the plow are being reduced to a minimum. HARSHBERGER has contributed much to this record, and has lately investigated[20] the plant formations on a series of cliffs, known as the Nockamixon Rocks, on the Delaware River in Pennsylvania. Upon the talus a climax mesophytic forest has developed, characterized by the beech, maple, and associated forms, with an oak forest upon the crest of the cliffs and a mixed one upon the larger rock shelves.

More recently he has studied the Navesink Highlands[21] upon the coastal plain of New Jersey. The forest is here dominated by the chestnut and the chestnut oak, with a more xerophytic association at the summit, characterized by dwarfed trees placed at wide intervals.—GEO. D. FULLER.

Plant remains in Scottish peat mosses.—LEWIS has published a fourth paper[22] upon this subject, the present investigation dealing with the Scottish Highlands and Shetland. An appendix also discusses the Icelandic peat deposits. His former conclusions as to the principal stages in the history of vegetation over peat-covered areas, since the later stages of the glacial period, were abundantly confirmed. The stages are as follows: (1) an arctic-alpine

[19] FISCHER, HUGO, Licht- und Dunkelkeimung bei Farnsporen. Beihefte Bot. Centralbl. **27**[1]:60–62. 1911.

[20] HARSHBERGER, JOHN W., The plant formations of the Nockamixon Rocks, Pennsylvania. Bull. Torr. Bot. Club **36**:651–673. 1909.

[21] ———, The vegetation of the Navesink Highlands. Torreya **10**:1–10. 1910.

[22] LEWIS, FRANCIS J., The plant remains in the Scottish peat mosses. Part IV. Trans. Roy. Soc. Edinburgh **47**:793–833. *pls.* 5. 1911.

vegetation on the moraine deposited by the last ice sheet; (2) a forest of birch and hazel; (3) a layer of arctic-alpine plants, occurring down to sea level in Shetland; (4) a forest of pine, hazel, and birch, occurring up to 3200 feet; (5) a layer of peat, accumulated from stage 4 to the present day, consisting entirely of moorland plants. This means an alternation of two forest beds with two arctic beds, before the peat came in.—J. M. C.

The structure of Mesoxylon.—In 1910, SCOTT and MASLEN published *Mesoxylon* as a new genus of Cordaitales, which included five species. One of these, *M. Sutcliffii*, has now been studied by MASLEN,[23] so far as the structure of stem and leaf is concerned. The name of the genus refers to the fact of its intermediate position between *Cordaites* and *Poroxylon*, and the known species appear to bridge the gap almost completely. The present study confirms this original conclusion, the particular species studied being much nearer to *Cordaites* than *Poroxylon*. A condensed summary is given of the resemblances of *M. Sutcliffii* to each of these genera, and also its differences in each case. One of the most interesting features of *Mesoxylon* is that it illustrates the gradual extinction of centripetal wood and the establishment of endarch structures in the *Cordaites*.—J. M. C.

The chromosomes of Dahlia.—ISHIKAWA[24] finds 16 and 32 chromosomes in *Dahlia coronata*, but 32 and 64 in nine other species and races. In the pollen mother cells of *D. coronata* in the heterotypic prophase, the chromosomes are paired, but in the other species the pairing is seen also at the homotypic mitosis, indicating, according to ISHIKAWA, that the vegetative cells of these species are tetraploid.

From the literature and his own observations, the reviewer has tabulated the number of chromosomes in more than 30 species of composites, and finds that the number varies from 3–6 in *Crepis virens* to 21–42 in *Hieracium flagellare*, with 8–16 or 9–18 as the most usual numbers. The extraordinary variety of form in Compositae may be related to the variation in the chromatin.—CHARLES J. CHAMBERLAIN.

Proteolytic enzyme of Drosera.—The proteolytic enzyme of four species of *Drosera* (*D. auriculata*, *D. Menziesii*, *D. peltata*, *D. Whittakeri*) has been investigated by Miss JEAN WHITE,[25] who finds a pepsin-like enzyme present in all of them, but unassociated with any peptolytic or tryptic enzyme. Peptic digestion occurred either in acid, basic, or neutral medium, every test giving a good biuret reaction for peptones; but in no instance could the faintest trace of amides be found with the tryptophane reaction. This dis-

[23] MASLEN, ARTHUR J., The structure of *Mesoxylon Sutcliffii* (Scott). Ann. Botany **25**:381–414. *pls. 33–36*. 1911.

[24] ISHIKAWA, M., Cytologische Studien über Dahlien. Bot. Mag. Tokyo **25**:1–8. *pl. 1*. 1911.

[25] WHITE, JEAN, The proteolytic enzyme of *Drosera*. Proc. Roy. Soc. London B **83**:134–139. 1911.

covery is interesting, since it is the only record of a peptase occurring in plants unassociated with ereptase. The enzyme is present as such, not in the form of zymogen. The leaves of *Drosera* were found to be capable of absorbing dissolved peptones from liquids placed on their surfaces in a few hours.—CHARLES A. SHULL.

Hepaticae in Scotland.—MACVICAR[26] has published a full account of the liverworts of Scotland, stating that "this work may be regarded as a new departure for Scotland in this branch of botany," previous publications having been fragmentary. An ecological discussion of nearly 50 pages precedes the list, the latter including a full list of stations under each species. Among other interesting facts of distribution, the altitudes to which species ascend may be mentioned. Of the 225 species included in the list, 20 ascend above 4000 ft., 61 reach 3000–4000 ft., and 32 reach 2000–3000 ft.; which means that half of the Scottish species ascend above 2000 ft. There are 67 genera recognized in the list, those including 10 or more species being *Lophozia* (26), *Scappania* (20), *Marsupella* (13), and *Cephalozia* (10).—J. M. C.

A cretaceous Pityoxylon with ray tracheids.—It has been supposed that the occurrence of ray tracheids in the pinelike conifers is more recent than the Cretaceous, so that their discovery by BAILEY[27] in a *Pityoxylon* from the Upper Cretaceous of New Jersey is one of considerable interest. The species represents a structure intermediate between the older cretaceous pines and the most primitive of living pines; and the infrequent occurrence of ray tracheids in the older portions of the stems and their entire absence from the younger wood are taken to indicate that these structures are of recent origin and are not strongly fixed upon the plant. This shifts the development of ray tracheids from the Tertiary to the Upper Cretaceous.—J. M. C.

Longevity of seeds.—Miss REES[28] has made a study of the relation existing between the structure and permeability of the coats and the longevity of seeds. In general, the macrobiotic seeds (retaining vitality for more than 15 years) belong to the legumes and have highly cutinized coats. *Eucalyptus calophylla* and *E. diversicolor* are exceptions. They possess no impervious covering, and, contrary to the general situation for macrobiotic seeds, they are large and very rich in oils.—WILLIAM CROCKER.

Laboratory air.—NELJUBOW[29] has studied the growth of the pea seedling in laboratory air and comes to the following conclusions: Ethylene is the

[26] MACVICAR, SYMERS M., The distribution of Hepaticae in Scotland. Trans. and Proc. Bot. Soc. Edinburgh **25**:vi+336. 1910.

[27] BAILEY, I. W., A cretaceous *Pityoxylon* with marginal tracheids. Ann. Botany **25**:315–325. *pl. 26*. 1911.

[28] REES, BERTHA, Longevity of seeds and structure and nature of the seed coat. Proc. Roy. Soc. Victoria N.S. **23**:393–414. 1911.

[29] NELJUBOW, D., Geotropism in der Laboratoriumsluft. Ber. Deutsch. Bot. Gesells. **29**:97–112. 1911.

effective impurity of the laboratory air. Acetylene in sufficient concentration has the same effect. In these impurities the seedling loses its negative geotropism and becomes transversely geotropic or diageotropic. All his conclusions, with much more data for substantiation than NELJUBOW has, were reported by KNIGHT and his co-workers at the Boston meeting of the A.A.A.S. in 1910. Extracts of this report appear in *Science*[30] and in the *Experiment Station Record*.[31]—WILLIAM CROCKER.

Height of the Douglas fir.—Inquiring into the cause of the great height of the Douglas fir, FRYE[32] finds that unusual size is a characteristic of many of its neighbors, and cites as an example the common brake, which in this region attains a height of 14 feet. This among other things leads to the supposition that the cause of such giants of vegetation is to be sought in the climate, and hence to the conclusion that the fir is tall because it grows in a damp climate and in conditions of partial darkness due to overcrowding and to the large number of dark days during its elongating season.—GEO. D. FULLER.

The chromosomes of Ginkgo.—Conflicting accounts by CARDIFF, CAROTHERS, and SPRECHER regarding the number of chromosomes in *Ginkgo biloba* led ISHIKAWA[33] to examine the readily accessible Japanese material. He found 12 bivalent chromosomes in the pollen mother cell, the number reported by CARDIFF. One of the 12 is constantly larger than the other 11, a fact recorded in the figure but not in the text of both CARDIFF and CAROTHERS. While the paper is short, the evidence that 12 is the gametophytic number of chromosomes in *Ginkgo* is conclusive.—CHARLES J. CHAMBERLAIN.

The embryo sac of Pandanus.—From material of *Pandanus coronatus* collected in Java, CAMPBELL[34] finds that the embryo sac has a nearly normal egg apparatus, an endosperm nucleus formed by the fusion of two or more nuclei, and a considerable mass of antipodals, resembling the antipodal situation in *Sparganium*, except that in *Sparganium* most of the antipodals are formed after fertilization. CAMPBELL had already noted as many as 14 nuclei in the embryo sac of *Pandanus* before fertilization.—CHARLES J. CHAMBERLAIN.

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[30] KNIGHT, LEE I., ROSE, R. CATLIN, and CROCKER, WILLIAM, Effect of various gases and vapors upon etiolated seedlings of the sweet pea; a new method of detecting traces of illuminating gas. Science N.S. **31**:635, 636. 1910.

[31] Exp. Sta. Rec. **23**: 229, 230. 1910.

[32] FRYE, T. C., Height and dominance of the Douglas fir. Forestry Quart. **8**: 468–470. 1910.

[33] ISHIKAWA, M., Ueber die Zahl der Chromosomen von *Ginkgo biloba* L. Bot. Mag. Tokyo **24**:225, 226. *figs. 3.* 1910.

[34] CAMPBELL, D. H., The embryo sac of *Pandanus coronatus*. Bull. Torr. Bot. Club **38**:293–295. 1910.

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